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Contents

Page

A Systematic Study of the Main Arteries in the Region of the Heart—Aves XI. Tinamiformes—With some Notes on their Apparent Relationship with the Galliformes—*Fred H. Glenny* - - - - - - - - - - - - - 31

Protein and Fat of the Salmon Egg as Sources of Energy for the Developing Embryo—*A. Hollett and F. R. Hayes* - - 39

The Effects of Variations in Atmospheric Pressure upon Insects—*W. G. Wellington* - - - - - - - - - - - 51

Parasites, Diseases, Injuries, and Anomalies of the Columbian Black-tailed Deer, *Odocoileus hemionus columbianus* (Richardson), in British Columbia—*Ian McTaggart Cowan* 71

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A SYSTEMATIC STUDY OF THE MAIN ARTERIES IN THE REGION OF THE HEART—AVES XI.

TINAMIFORMES—WITH SOME NOTES ON THEIR APPARENT RELATIONSHIP WITH THE GALLIFORMES[1]

BY FRED H. GLENNY

Abstract

Five species of tinamous were dissected and diagrams of the arteries in the neck and thorax prepared. All species were bicarotidinae normales, and each presented both a right ligamentum botalli as well as a ligamentum aortae. An arteria pericardia was present in one species. Similarities and dissimilarities in structure of the tinamous and gallinaceous birds are discussed with reference to possible phylogenetic relationships. Considerable similarity in arrangement-patterns of these two orders of birds exists and may be based upon structural characteristics of common origin, rather than upon an instance of parallel development. Tinamous may have a more recent origin from the ancestral form than their apparent relatives the Galliformes.

Introduction

During the past century, the tinamous have evoked considerable interest, especially with reference to their position in the class Aves. During the early to middle part of the 19th century, they were classified with the gallinaceous birds. Later on, in the latter part of the 19th and early part of the 20th centuries, they were placed in a separate order, but still in close association with the gallinaceous birds. Such arrangements in classification probably were due, in part, to the many gross similarities in structure exhibited by the tinamous and gallinaceous birds. At the same time, however, the tinamous were known to have several characteristics more typical of certain other primitive birds such as the kiwi and strutheous birds. As a result, considerable difficulty has been encountered in placing them in a phylogenetic series. This perhaps is due more to their retention of primitive or reptiloavian characteristics than to other factors.

Those extant forms that present the more primitive structural characteristics are not, de facto, remnants of an early ancestral form of bird life, but are probably more recently divergent groups from the more primitive ancestor, and, as a result, have retained many more of the basically primitive (reptiloavian) characteristics of the less rapidly evolving (more primitive) ancestral forms. To this same point may be added the observation that the more

[1] *Manuscript received in original form, August 31, 1944, and as revised, February 6, 1945. Contribution from the Department of Zoology, University of Toronto, Toronto, Ont.*

highly divergent groups (with reference to forms that may be presumed to have had a common primitive avian or reptiloavian origin) arose at a much earlier time, or lower from the main stem, and that early divergent trends in evolution may well account for the ultimately wide differences in the extant forms within an order or subclass of animals.

Finally, it may well be concluded that families of birds (or other animals) that present highly uniform characteristics (structural) may be considered as terminal or end-line forms in any phase or trend of evolution. Such a condition is found to exist in a few families of the Passeriformes (8). For the most part, however, the evolution of an order or family of birds is a continuous and gradual process. Thus evolution with its multiple series of divergences may proceed along not one, but several lines of structural change simultaneously. This is a general observation, but, as in the Comsothlypidae (8), a more generally uniform rate of evolution appears to have taken place with the result that the important family characteristics have become highly uniform and well-defined in nature. This does not, however, appear to be entirely the case in the Tinamidae as will be noted in part in this paper.

Beddard (1) appears to have had somewhat the same idea with regard to ordinal evolution, for in 1898 he made the following observations:

"The Galli seem to be undoubtedly an ancient group of birds, a view which is upheld by their points of likeness to many diverse groups.

"That they are an ancient group is also shown by their quintocubitalism, the primitive character of the gut convolutions, the often complete muscle formula, and the existence of basi-pterygoid processes. Less weight, however, appears to be due to these more general points of resemblance than to other slighter but equally constant similarities. The existence of the entepicondyle-ulnaris muscle is an example to the point. The Galli share this muscle with the Tinami only; and no one will doubt on other grounds that the Gallinaceous birds and Tinamous are distinctly related."

Another observation by Beddard (1) that should be noted at this time is: ". . . Archaeopteryx must be regarded as a parallel branch to the existing birds, and not as their ancestor." Such a point of view is of interest in light of previous studies of the present writer. In these studies, many apparent instances of parallel development of the arterial arrangement are readily observable.

In 1855, Reichenbach (9) placed the tinamous and gallinaceous birds in the same Order (*Gallinae*). This order was divided into three families—Sandhühner (Syrrhaptidae), Hühner (Gallinaceae), and Stutzhühner (Crypturidae). The general external features and appearance of the tinamous led to the placing of the genera *Tinamus* and *Bonasa* together with the other Syrrhaptidae.

That such a classification appeared reasonable, at that time, may be better understood when one considers the fact that not too much was known of the anatomy of these forms during that period, and the mounted and skin speci-

mens of these two genera bear considerable resemblance to each other. The Phasianidae, however, were placed in the family Gallinaceae, probably owing to their differences in external appearance—at least in so far as *Bonasa* is concerned. Since no great amount of systematic or comparative anatomical studies had been carried out at that time, it is easy to understand that such mistakes in classification were made.

It was not until Professor W. K. Parker presented his *Osteology of the Gallinaceous Birds and Tinamous*, and Professor T. Huxley published his paper *On the Classification of Birds* that avian systematics began to have an adequate foundation based upon structural similarities. More recent work, particularly taxonomic and palaeontologic, has served to refine and further clarify probable relationships.

Evans (2) placed the tinamous and gallinaceous birds in separate orders, but in his system he placed the Tinamiformes just ahead of the Galliformes. It should be noted here that Evans also included the Gruiformes, further separated by Wetmore (10) and others, with the Galliformes. Evans then goes on to note: ". . . the pterylosis and the habits generally (of the Tinamous), are Galline.".

There are, naturally enough, several points of similarity as well as dissimilarity in structure between the Tinamiformes and their presumed allies the Galliformes. Some of these may well be summarized at this time.

POINTS OF SIMILARITY	TINAMIFORMES	GALLIFORMES
1. Oil gland	Tufted	Tufted, nude, or lacking
2. Remex V	Present	Present
3. Leg muscles	*ABXY* present	*(A)BXY* present
4. Entepicondylo-ulnaris	Present	Present
5. Extrinsic muscles of trachea	Sometimes 2 pairs	Sometimes 2 pairs
6. Internal carotid (trunk) arteries	Two	Two
7. Crop	Present and large	Present and large
8. Gall bladder	Present	Present
9. Expansor secundariorum	Present	Present
10. Caeca	Present (well developed)	Present
11. Incubation period	About three weeks	18 to 28 days
12. Hallux	Elevated or wanting	Elevated
13. Sternum	Well-developed keel	Well-developed keel
14. Wings	Short; concave and rounded	Short and rounded
15. Primaries	10	10
16. Secondaries	13 to 16	12 to 19
17. Down	Present on nestling	Present on nestling
18. Tensor patagii tendon	Broad diffuse band	Broad diffuse band
19. Coracoid	Jointed, not fused with scapula	Jointed, not fused with scapula
20. Habits	Essentially ground birds: feeding habits are essentially the same—seeds, fruits, grain, berries, small larvae, and bugs	

POINTS OF DISSIMILARITY		
1. Skull (vomer and palatine bones)	Dromaeognathous	Schizognathous
2. Pelvis (ischium and ilium)	Completely fused Bones free distally	Not fused Fused posteriorly
3. Suprasciatic muscle	Present	Absent
4. Tongue	Small and triangular	Sagittate
5. Furcula	U-shaped	Y-shaped

POINTS OF DISSIMILARITY	TINAMIFORMES	GALLIFORMES
6. Quadrate bone	Single head	Double head
7. Pygostyle	Absent	Present
8. Aftershaft	Rudimentary or wanting	Large except in *Pavo*
9. Incubation	By male	By female
10. Sternum	Long and slender	Shorter and broad

Garrod (3) noted that in the tinamous, both internal carotid (trunk) arteries (referred to at that time as common carotid arteries) were present and entered the hypapophysial canal to pass anteriorly to the head without fusing into a single trunk artery. Confirmation of this observation is made in the observations of this paper.

Materials

Two specimens of *Eudromia elegans* d'Orbigny & Geoffroy (#18956 and #227552) and single specimens of *Tinamus m. major* (Gmelin) (#320032), *Nothoprocta perdicaria* (Kittlitz) (#19856), *Nothura maculosa boliviana* Salvadori (#227165), and *Crypturellus* sp./*Crypturornis* [= *Crypturus*] sp. (#321586) were dissected and diagrams of the main arteries in the region of the neck and thorax prepared.

Materials used in this study were from the alcoholic collection of the United States National Museum. The numbers following the species names refer to the number of the specimens that were used.

Observations

The basic ordinal arterial arrangement-pattern of the tinamous (as based on the present studies) is simple. Both internal carotid (trunk) arteries (*24*) are present and enter the hypapophysial canal, along which they pass to the head. The common carotids (*8*) give rise to the vertebral (*21*) and superficial cervical (*22*) arteries. The scapular arteries (*23*) arise as branches of the superficial cervicals, while the syringotracheal (*19*) and basioesophageal (*20*) arteries arise as very small branches of the vertebral artery (except in *Nothoprocta* where they may arise from the common carotid). The ductus shawi (*18*) arises either from the vertebral or common carotid artery. In general, the subclavian arteries (*9*) give rise to the coracoid major (*10*), axillary (*12*), intercostal (*13*), and two pectoral (*14*) arteries in order, but in *Crypturellus*/*Crypturornis* the intercostal may be found as a lateral branch of the coracoid major. The coracoid minor (*11*) when present arises as a branch of the axillary artery.

The ligamentum aortae (*5*) remains as a remarkable vestige of the embryonic left radix aortae. The right ligamentum botalli (*6*), however, persists in various degrees from readily visible to nearly invisible, or it may become entirely fused with the right radix aortae (*4*) or even completely atrophied. In *Tinamus m. major* (Fig. 1) and *Nothoprocta perdicaria* the ligamentum botalli (*6*) may be observed to retain its proximal as well as its distal attachments, while in the other three species the proximal attachment is lacking (Figs. 2 and 3).

Origin of the thyroid artery (*17*) varies from the common carotid artery in *Tinamus* and *Nothoprocta* to the superficial cervical artery in the other species that were dissected.

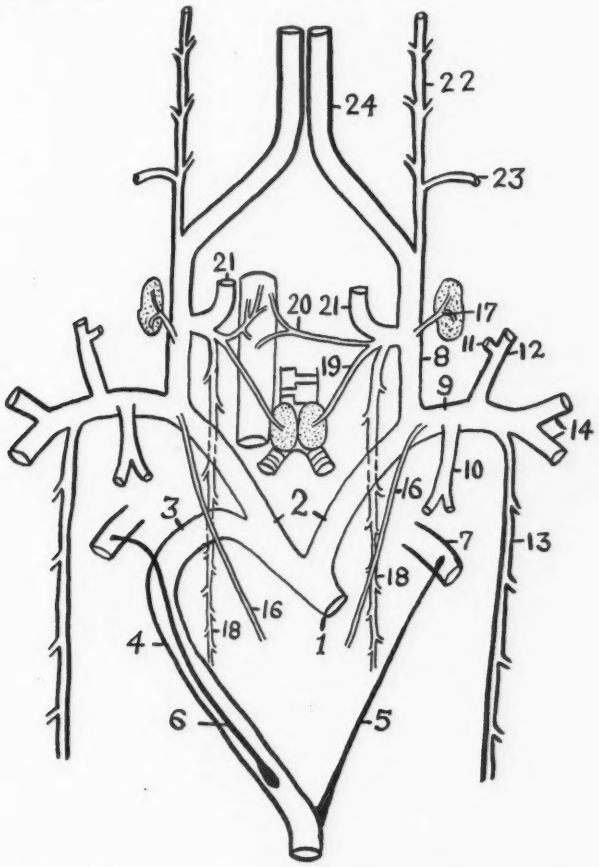

FIG. 1. *Diagram of main arteries in the neck and thorax of Tinamus m. major. Ventral view.*

KEY TO ABBREVIATIONS (Figs. 1 to 3)

(*1*) Aortic root; (*2*) innominate arteries; (*3*) right fourth aortic arch; (*4*) right radix aortae; (*5*) ligamentum aortae; (*6*) ligamentum botalli; (*7*) pulmonary artery; (*8*) common carotid artery; (*9*) subclavian artery; (*10*) coracoid major artery; (*11*) coracoid minor artery; (*12*) axillary artery; (*13*) intercostal artery; (*14*) pectoral arteries; (*15*) myocutaneous artery; (*16*) pericardial artery; (*17*) thyroid artery; (*18*) ductus shawi; (*19*) syringotracheal artery; (*20*) basioesophageal artery; (*21*) vertebral artery; (*22*) superficial cervical artery; (*23*) scapular artery; (*24*) internal carotid (trunk) artery.

In *Eudromia* a paired superficial or external myocutaneous artery was observed. This vessel arose from the subclavian artery just medial to the two pectoral arteries.

Tinamus m. major may present a small artery (arteria pericardia) (*16*), which arises from the innominate artery (*2*) at the point of origin of the common carotid and subclavian arteries. (A somewhat similar artery was described by the author in an earlier paper (7).)

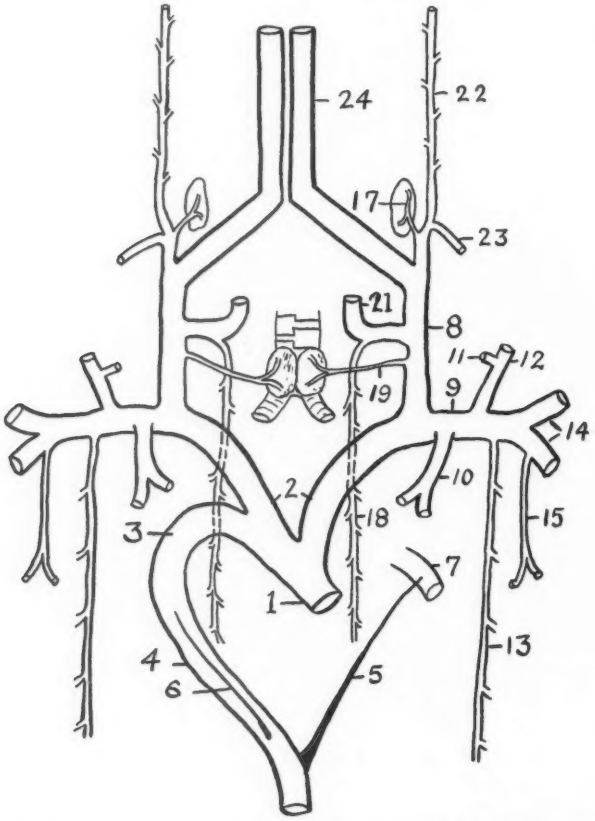

FIG. 2. *Diagram of main arteries in the neck and thorax of Nothura maculosa boliviana. Ventral view.*

A small myocutaneous artery (somewhat similar to that found in *Eudromia*) is present in *Nothura maculosa boliviana* (Fig. 2). This vessel arises from the posterior pectoral artery, or from the subclavian artery, and supplies the skin and some of the muscles in the dorsolateral part of the thoracic region.

Discussion

The major blood vessels of the specimens studied form a fairly characteristic ordinal arrangement-pattern. It may be noted, however, that there are a few different vessels present in two or three species. This might be

regarded as evidence of reasonably recent divergence from the more primitive ancestral form. It is obvious that evolution among the tinamous has not progressed to the same extent as is evidenced by the various members of the

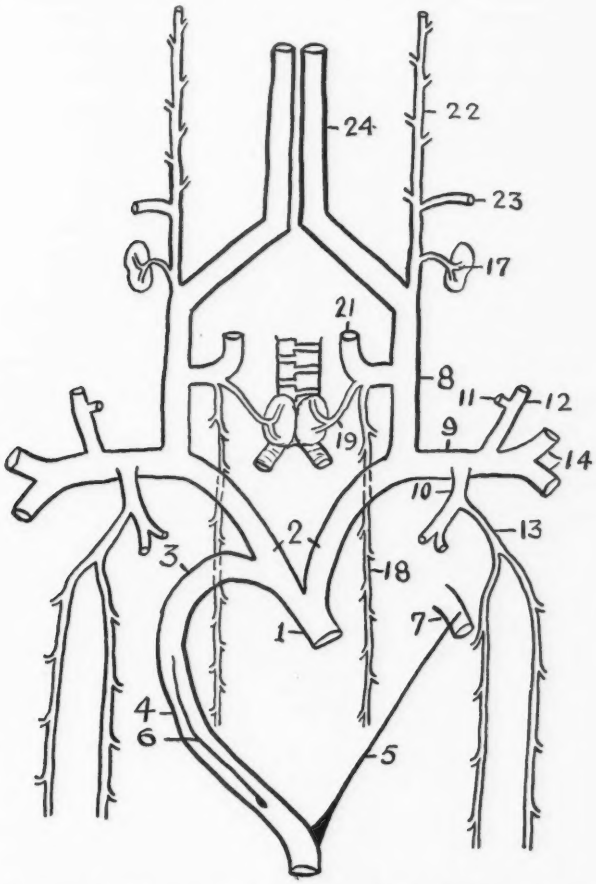

FIG. 3. *Diagram of main arteries in the neck and thorax of Crypturellus/Crypturornis sp. Ventral view.*

several families of the Galliformes. In due time, however, should the present lines of apparent vascular changes continue, variation in arterial arrangement might well become as diverse and varied as is presently notable among the Phasianidae.

Except for the differences in the points of origin of the vertebral artery and the presence or absence of one or two secondary vessels, the basic ordinal arterial arrangement-patterns of the Tinamiformes and the Galliformes are

very similar. While these similarities may be accounted for by the anomaly of parallel development, the large number of dissimilarities in the arterial arrangements when the tinamous are compared with *Apteryx* (4), *Rhea* (6), *Dromaeus*, and *Casuarius* (5) cannot be completely discounted in a consideration of characteristics upon which a phyletic or taxonomic system may be based. It would appear, therefore, that, based upon the single factor of basic ordinal arterial arrangement-patterns in addition to the characteristics listed previously in this paper, the tinamous show closer anatomical relationships to the Galliformes than to most other orders of extant birds.

Acknowledgments

The writer wishes to express his gratitude to Dr. Alexander Wetmore and Dr. Herbert Friedmann, United States National Museum, for making available the materials used in this study, and to Dr. Harry C. Oberholser, Cleveland Museum of Natural History, for his helpful suggestions in the preparation of this paper.

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PROTEIN AND FAT OF THE SALMON EGG AS SOURCES OF ENERGY FOR THE DEVELOPING EMBRYO[1]

By A. Hollett[2] and F. R. Hayes[3]

Abstract

An egg weighing 130 mgm. starts off with 25 mgm. of protein, of which 45% is consumed for energy up to the time of complete yolk sac absorption; for fat the corresponding figures are 9.4 mgm. and 77%. Up to the time of hatching there is no measurable decrease in either protein or fat, although recorded respiratory measurements suggest a probable loss of some 0.6 mgm. of fat. The dried embryo, when the yolk is gone, weighs 17.3 mgm. Expressed as calories, 41% of the yolk becomes living embryo and the rest is used up for metabolic purposes. Carbohydrate plays no appreciable part as an energy source. Non-protein nitrogen increases steadily throughout development, being stored in the embryo. The carbohydrate, protein, fat sequence of energy sources, said to be of general application, could not be demonstrated; a more likely one is fat, protein, fat, protein.

The first two papers of this series (11, 9) were concerned with investigations of fat and carbohydrate metabolism of the embryonic salmon. The storage and utilization of protein remained to be measured, so the present study was undertaken. With an assessment of the part played by the third great class of foodstuffs it becomes possible to make a comparison of the relative contributions of the energy sources to storage and combustion; to state the calorific cost of making an embryo out of yolk and the efficiency of the process; and to see whether the sequence of energy sources during development follows the course reported for other forms such as the chick.

In what follows, the word "larva" is used to describe the embryo with its attached yolk sac both before and after hatching. The larval stage is said to end when the yolk sac has disappeared, at which time our observations also terminated.

Methods

Eggs from three individual Atlantic salmon (*Salmo salar*) were fertilized on the same day and segregated in three pairs of trays in the Government Fish Hatchery, Bedford, N.S. Batch one was soon brought to the university and reared in a small hatchery; batches two and three were brought in successively at later dates. As the Government hatchery is several degrees cooler than the university hatchery, the three batches hatched at widely separated dates. On the basis of a study of temperature coefficients (10), analytical data, and morphological stages (15), it has been possible to adjust the ages of the three batches and pivot them around a zero day or central

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[3] *Associate Professor of Zoology.*

date of hatching, in this case 46 days after fertilization. Ages are thus expressed as the number of days before and after hatching (1, 11).

No food was supplied the young salmon at any time. Weekly estimations of protein were made of the eggs and larvae, as well as of the egg fractions, embryo, yolk, and capsule. The same estimations were made of some unfertilized eggs. The original results have been corrected to apply to a developing egg of 130 mgm. wet weight. Thus when the wet weight averaged 115.6 mgm. results were multiplied by the factor $130/115.6 = 1.13$.

During the prehatching period 15 to 20 eggs were taken for each test. They were rolled between filter paper to remove adherent water, weighed, hydrolysed with concentrated sulphuric acid in a small Kjeldahl flask for three hours, and made up to 100 ml. On shaking, the solution was quite homogeneous, and provided 1 ml. portions on which nitrogen was estimated by the micro-Kjeldahl technique. In quadruplicate analyses the probable error was always less than $\frac{1}{2}\%$. A digestion mixture of three parts concentrated sulphuric acid and one part concentrated phosphoric acid was used (12). The method is rapid and trouble-free. In distillation the ammonia was received in 2% boric acid solution, which held it without interfering with the subsequent titration against acid, in which B.D.H. 4460 indicator was used.

In the estimation of non-protein nitrogen 50 eggs were ground with a little distilled water, and the protein precipitated by a modification of the method of Folin and Wu (4) in which sulphuric acid and sodium tungstate are used. Nitrogen was estimated on an aliquot of the filtrate. This, as non-protein nitrogen, was subtracted from total nitrogen to give protein nitrogen.

It is probable that yolk protein differs from that of the embryo, and it was to be expected that, due to a variation in amino acids, a different factor for the conversion of nitrogen to protein would have to be applied in each case. It was therefore necessary to make determinations of the percentage of nitrogen in the pure protein of yolk and embryo. For the purpose, 150 yolks were ground with anhydrous sodium sulphate to absorb all moisture, and the mixture extracted with ether in a Soxhlet apparatus for five hours, followed by alcohol extraction for six hours. The purpose of the alcohol was to remove certain phospholipids and lipid fractions attached to protein, which are not taken out by ether. Sodium sulphate and the remaining non-protein components were removed by slowly siphoning some 5 litres of boiling water into the thimble still contained in the Soxhlet apparatus. It was assumed that the end product of these operations was protein only. This was dried at 103° C. for several days and the nitrogen estimated on about 0.7 mgm. Protein divided by nitrogen equals protein factor, which, for yolk eight days before and eight days after hatching, varied from 6.33 to 6.46 with an average of 6.4. Sufficient embryonic protein for the foregoing procedure was obtainable only when the yolk was almost completely absorbed. Duplicate analyses gave an average embryo factor of 6.75.

By this method there is enough yolk to determine a yolk factor only in the earlier stages of development while an embryo factor can only be determined

in later stages when the embryos have reached a certain size. Application of factors thus rests on the assumption that the percentages of nitrogen in yolk protein and embryonic protein, respectively, are constant throughout development. This supposition is supported by our analyses of yolk sacs from the beginning up to some time after hatching, during which no significant variation could be found. At the beginning, whole eggs were used, and these included the capsule, but since the capsule represented less than 10% of the total protein and had a factor of 6.55 (20), its inclusion would make little change in the yolk factor. Whether the nitrogen content of the salmon embryo remains constant is not known, but such an assumption is not unreasonable in view of the fact that Cahn (cited in 13, p. 1063) found that the percentage of nitrogen in the pure protein of chick embryos did not vary with development.

In the section following it is stated that there was no directly measurable decline in protein before hatching. Such a result does not depend on choice of a factor and would still hold true if values had been expressed directly as nitrogen.

Through the centre part of development use was made either of direct protein estimates or those derived from such relationships as:

larva minus yolk equals embryo.

In earliest and latest stages when the embryo and yolk were, respectively, very small, only the direct method was reliable. Most of the values in Table I represent both methods.

The Interval before Hatching

The probable loss in dry weight before hatching can be estimated from the oxygen consumption by assuming the general relationship in which 1 gm. of protein corresponds to 0.95 litres of oxygen; of fat, to 2.02 litres; and of carbohydrate, to 0.81 litres. Carbohydrate need not be further considered since it is a small fraction of the egg and increases during development (9). Privolniev (16) measured the oxygen consumption of salmon eggs at three-day intervals, expressing the results in cu. mm. per 35 embryos per hour. When his values are multiplied by the number of hours in each interval, divided by 35 and summed up, it is found that one egg used 2840 cu. mm. of oxygen from fertilization to hatching. A correction is made necessary by the fact that measurements were made at 10° C. while the eggs were reared at a lower, unspecified temperature. They actually hatched in 68 days, while at 10° they probably would have hatched in something like 47 days (Embody (3) on brook trout eggs). The corrected value is therefore

$$\frac{2840 \times 47}{68} = 1960 \text{ cu. mm.},$$

which is probably maximal because the eggs would not be acclimated to the higher temperature before measurement. Making use of it, however, it is calculated that $1960 \div (2.02 \times 10^3) = 0.97$ mgm. fat loss, or $1960 \div (0.95 \times 10^3) = 2.06$ mgm. protein loss would occur from the egg.

TABLE I

RESULTS OF ANALYSES OF EGGS AND EGG FRACTIONS. ALL FIGURES ARE IN MGM. PER 130 MGM. EGG

1	2	3	4	5	6	7
Days before and after hatching	Non-protein nitrogen			Protein in embryo (N × 6.75)	Protein in yolk (N × 6.4)	Protein in larva
	Embryo	Yolk	Larva			
−43		0.08	0.08		24.2	24.2
−36		0.08	0.08		24.2	24.2
−33		0.08	0.08	0.21	23.6	23.8
−28		0.085	0.085	0.30	23.7	24.0
−22	0.003	0.085	0.090	0.61	23.5	24.1
−19	0.005	0.085	0.09	0.90	22.7	23.6
−17	0.005	0.085	0.09	1.16	22.7	23.9
−15	0.006	0.085	0.09	1.35	22.9	24.0
−12	0.007	0.085	0.09	1.51	21.9	23.4
−11			0.1			
− 8	0.01	0.085	0.1	2.27	22.0	24.3
− 6			0.11			
− 4	0.015	0.085	0.1	3.12	21.1	24.2
0	0.02	0.08	0.1	3.58	20.4	24.0
2	0.02	0.08	0.1	4.28	20.0	24.3
3	0.024	0.081	0.105			
6	0.03	0.075	0.105	4.31	20.2	24.5
12	0.045	0.06	0.107	4.76	18.6	23.4
15	0.05	0.05	0.108			
18	0.055	0.052	0.11	5.27	18.2	23.5
23	0.063	0.048	0.11	6.04	15.6	21.6
34	0.08	0.038	0.115	7.22	13.3	20.5
43	0.094	0.032	0.118	8.07	9.94	18.0
45	0.10	0.033	0.12			
56	0.113	0.02	0.124	11.4	4.06	15.5
65	0.124	0.007	0.127	12.6	0.81	13.4
67			0.13			

In the rainbow trout (*Salmo irideus* or *Trutta iridea*) the total oxygen consumed up to the time of hatching (at 10.31°) is obtainable from data by Schlenk (17), and works out at some 700 cu. mm. Schlenk gives no egg weights, but if the trout egg be taken to weigh half as much as the salmon egg the value for salmon would be 1400 cu. mm. of oxygen, corresponding to a utilization of 0.7 mgm. of fat or 1.5 mgm. of protein. Applying the same treatment to Schlenk's carbon dioxide analyses it is found that in the trout about 470 cu. mm. are produced to hatching, which gives in the salmon a consumption of

$$\frac{470 \times 2}{1.54} = 0.6 \text{ mgm. of fat}$$

or

$$\frac{470 \times 2}{0.76} = 1.2 \text{ mgm. of protein.}$$

Schlenk's respiratory quotients would indicate fat utilization—in fact they are too low even for pure fat. Amberson and Armstrong (2) report similarly low respiratory quotients (R.Q.) for *Fundulus* eggs.

From respiration studies therefore it appears that, as a minimum, 0.6 mgm. of fat or 1.2 mgm. of protein have to be accounted for as used up before hatching. These amounts represent 7% of the fat (11) or 5% of the protein present at the start (Table I), or some combination thereof. Direct analyses have failed to demonstrate any clear prehatching diminution in dry weight (7), fat (11), or protein (this paper). It must therefore be concluded that owing to normal weight variations from egg to egg, materials used up fall within the limits of experimental error when attempts are made to measure them directly. We are inclined to think that the prehatching energy source is almost wholly fat for the following reasons:

1. The R.Q. of eggs is low.
2. The loss of weight, considered as fat, is minimal, and therefore most easily concealed in experimental error.
3. The total fat curve (11, Fig. 1) shows considerable fluctuation in the prehatching interval.
4. We have carefully examined our protein values and consider it unlikely that the necessary protein could have been consumed without discovery.

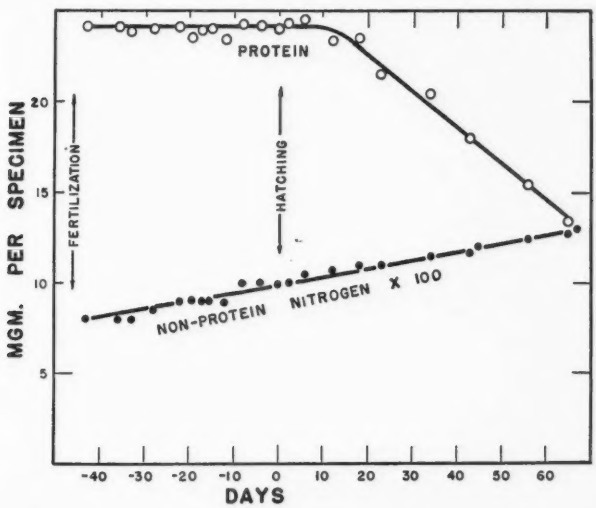

FIG. 1. *Upper curve, total protein of the larva. Lower curve, non-protein nitrogen of the larva.*

Total Protein of Larva (Embryo Plus Yolk)

The upper line of Fig. 1 and Column 7 of Table I gives the protein changes of the larva. An egg starts off with nearly 25 mgm. of protein of which nearly half is used up for energy by the end of the yolk period. Expressed as percentages the values indicate that at the beginning 23% of the wet weight and 62% of the dry weight of the larva is protein; by the time the yolk is

gone the values are 10% and 77% respectively. Outside of water protein is at all times the dominant constituent. A decline in protein is seen to begin shortly after hatching and to continue steadily thereafter. The decline is a measure of the protein used up as a source of energy.

The protein or total nitrogen of the salmonid system has been investigated several times. There has been a general failure to demonstrate any diminution up to hatching (19, 5, 6). The posthatching protein decline shown in Fig. 1 has also been observed by others (e.g., 6, Fig. 1). While all workers agree that a large amount of protein is used up for energy, the precise proportion reported is subject to variation, depending on whether the experiments (*a*) ended before all the yolk had gone, or (*b*) continued into the starvation period. From the following list it appears that the true value for protein used up at the completion of the yolk-sac stage lies in the vicinity of 40% of the original protein store.

Species	%	Reference
Salvelinus fontinalis	21.9	Gortner (5)
Salmo irideus	49.3	Smith (18)
Salmo salar	36.3	Hayes (6)
Salmo salar	44.6	This work

From time to time estimations were made of the nitrogen in the egg capsules, and these are shown in Table II. No trend can be noted. In analyses of whole eggs the average value of Table II was subtracted to give Table I, Column 7.

TABLE II

TOTAL NITROGEN OF EGG CAPSULES. ALL VALUES ARE IN MGM. PER 130 MGM. EGG

Days before hatching	Nitrogen	Days before hatching	Nitrogen
−43	0.376	−17	0.376
−35	0.37	−15	0.373
−28	0.376	− 4	0.376

Exchanges between Embryo and Yolk

Fig. 2 is a comparison of absorption from the yolk with storage by the embryo. It will be seen that the two curves are indistinguishable up to the time of hatching, following which there is a clear difference, representing combustion of protein. There is also an apparent flattening of the embryo curve at the time of hatching, similar to those previously described for fat (11) and carbohydrate (9).

Fig. 3, by turning the data of Fig. 2 into rates, answers the question: what per cent of its dry weight does the embryo absorb or store per day? The posthatching parts are based on the smoothed curves of Fig. 2. For the

prehatching parts, enlarged smooth curves, similar to Fig. 2, were made. Dry weights of embryos used in the calculations came, not from previous compilations, but from the protein values themselves. The dry embryo being 78 ± 5% protein, it is apparent that protein × 1.28 gives dry weight. In Fig. 3 we are plotting essentially $dy/y \,.\, dx$ against x, and as this gives a

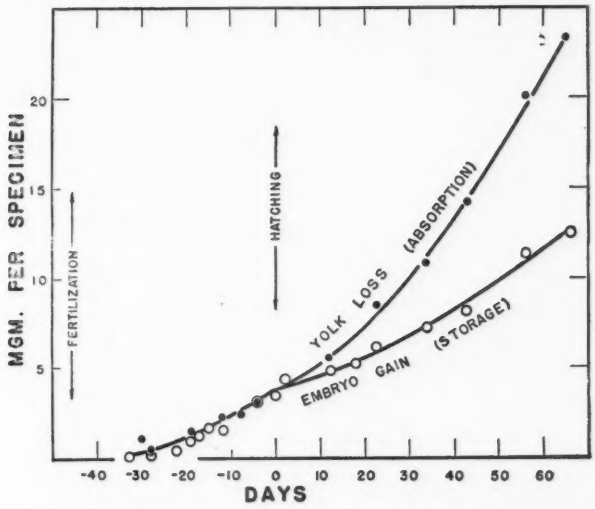

FIG. 2. *A comparison of protein absorption from the yolk with storage by the embryo.*

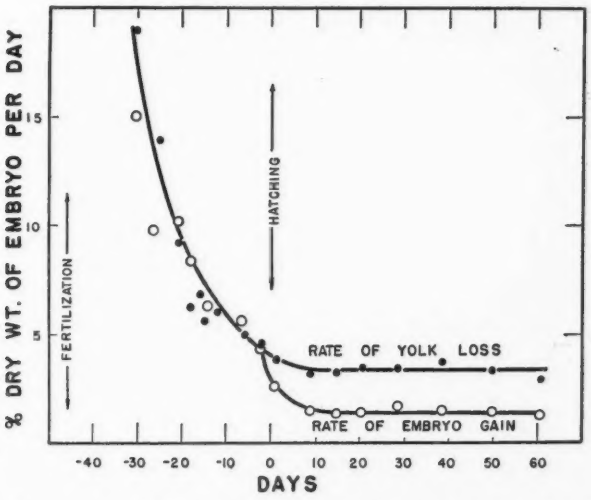

FIG. 3. *A comparison of the rate of protein absorption from the yolk with the rate of storage by the embryo.*

Minot or relative growth rate curve (8) it is not surprising to find that Fig. 3 exhibits the decline to whose general nature Minot drew attention. It is also obvious that, since protein is being used up and no food supplied, the yolk loss will be greater than the embryo gain. What could not be predicted is that the curves, once established, are parallel. The distance between the two lines is the rate of combustion and it is quite clear that no peak exists, which means that the larvae, in spite of marked increases in swimming as the yolk sac gets small, do not take protein for their extra activity. Previous work has shown a posthatching peak of combustion for fat (11, Fig. 4). On the other hand carbohydrate, or at any rate free carbohydrate, undergoes a steady increase in quantity during development (9).

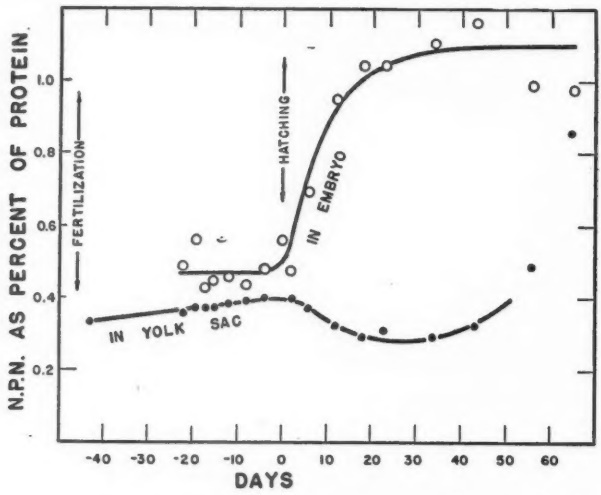

FIG. 4. *Changes in the concentration of non-protein nitrogen in embryo and yolk sac during development.*

Non-protein Nitrogen

Examination of Fig. 1 shows that the larval non-protein nitrogen increases steadily throughout development, which means either that excretory products are appearing faster than they are being carried away, or that free amino acids are appearing.

Fig. 4 shows that the new non-protein nitrogen is in the embryo rather than the yolk, for the embryo exhibits a marked increase after hatching. The salmon in this respect differs from the chick in which there is, after the fifth day of development, a steady fall in the ratio of non-protein nitrogen to protein (13, p. 1074).

The points on Fig. 4 indicate that the non-protein nitrogen of the yolk sac rises to a peak at hatching time, perhaps owing to the accumulation of excretory products which, after hatching, are eliminated. The posthatching

drop in non-protein nitrogen is reversed only in the final stages, where the apparent rise shown might be caused by the inclusion of membranes in the sample, for these, in the final samples, might represent an appreciable contamination of the yolk.

In a previous section it was indicated that, on respiratory evidence, if protein were a main source of energy before hatching, at least 1.2 mgm. would have to be used up. This would give rise to 0.19 mgm. of non-protein nitrogen, a quantity that might be held inside the capsule. The observed rise in non-protein nitrogen however (Table I, Column 4) is only 0.02 mgm. or 1/10th of the above, a fact that adds support to the idea that protein is not a main energy source before hatching. It must also be noted that Gortner (5) was unable to find any perceptible accumulation of nitrogenous end products in the prehatching phase of trout development.

Protein and Fat as Energy Sources

In a previous paper (11) the fat metabolism of the developing salmon was considered. The observations terminated "when the yolk sac had practically disappeared". With the original tables before us (they were not published) it has been a simple matter to extrapolate without great error to the point where the declining larval fat curve crosses the ascending embryo fat curve. The point occurs 64 days after hatching and gives a final value for embryo fat at 2.2 mgm. The latter, subtracted from the 9.4 mgm. present at the start, gives the fat consumed, namely 7.2 mgm. Taking the usual relations of 9.45 cal. per mgm. it is found that fat contributes 68 cal. to the energy requirements of the organism.

As to protein, it appears from Table I, Column 7, that 10.8 mgm. are used up which, at 4.25 cal. per mgm., represents 45.8 cal. contributed by protein.

The factors 9.45 and 4.25, which change mgm. of fat and protein into calories, are applicable to adult tissues. There is at present no way of telling how closely they describe yolk conversion.

The above relationships, with deduced gas exchanges, are brought together in the following list, from which it is seen that up to the end of the yolk sac period, the cost of constructing a salmon embryo is 114 cal., the larger portion coming from fat. (Carbohydrate (9) may be neglected.) The living embryo, when the yolk is quite gone, weighs about 120 mgm. so that each mgm. of living material costs just under 1 cal. The weight of a dried embryo being some 17 mgm., nearly 7 cal. are expended per mgm.

	Protein	Fat
Mgm. burnt up	10.8	7.2
Calories liberated	45.9	68.0
Oxygen consumed	10.3	14.3
CO_2 produced	8.2	10.2

In a general way the present results are like those previously reported, although close agreement is not to be expected because, as above mentioned, it is not easy to say exactly at what point to consider the yolk phase at an end. To minimize the difficulty, the protein and fat used up may be set down as a per cent of the total material taken for energy purposes. The results then are:

	Protein	Fat	Reference
Salvelinus fontinalis	63	37	Gortner (5)
Salmo irideus	84	16	Smith (18)
Salmo salar	60	40	This work

The efficiency of development may be obtained by comparing the calorific expenditure with the stored embryonic energy. The latter is obtained from our analyses as follows, each value representing the composition of one embryo from a 130 mgm. egg at the time the yolk is completely used up.

	Mgm.	Calories
Ash (unpublished data)	1.2	—
Protein	12.6	53.7
Non-protein nitrogen compounds	0.7	3.0
Fat (11)	2.2	20.8
Carbohydrate (9)	0.6	2.5
Total	17.3	80.0

The energetic result of development is thus 80 calories. It was seen above that the combustion represents 114 calories. The efficiency is therefore

$$\frac{80 \times 100}{114 + 80} = 41\%,$$

which represents living embryo, the remaining 59% going for osmotic work, secretion, circulation, etc. as well as for swimming in later stages.

Attempts have sometimes been made to divide the embryonic requirements into energy for (*a*) differentiation, (*b*) growth, (*c*) maintenance, and (*d*) extraneous activities such as swimming. All these possibilities and others are discussed by Needham (13, pp. 946–999), who shows that quantitative data are so far behind theory that little progress has been made. Our value of 41%, which is simply the ratio of output to input as used in industry, is known to embryologists as the apparent energetic efficiency. The efficiency of contracting mammalian muscle is generally given in texts as about 25%, while the efficiency of development of a frog embryo is 51, and a *Fundulus* embryo 53% (13, p. 968). Thus the salmon value, while higher than that for adult tissues, is below that previously reported for embryos.

The Sequence of Energy Sources

It has been suggested by Needham as a provisional generalization of chemical embryology that "during development, there is a succession of sources of energy, carbohydrate preceding protein and protein preceding fat" (13, p. 1656). The statement is somewhat modified in his later book (14, p. 603) in the light of respiratory measurements on amphibians and sea urchins. As to the salmon, we can see no clear evidence in support of the proposition. Carbohydrate, being continually on the increase, can hardly be a donor of energy. Reasons already given suggest that fat is the likely prehatching source, while half-way along the posthatching period a maximum of fat combustion is again reached (11). Before and after the latter the dominant source must be protein. Thus the sequence of dominant energy sources for the salmon appears to be: fat, protein, fat, protein.

It might be noted that R.Q.'s in the first stages of development are not very reliable because (*a*) the gas exchanges approach the limits of the methods and (*b*) there are likely to be initial rearrangements of pH involving carbon dioxide. Thus the first measurement of *Fundulus* R.Q. was 0.9 (2) while that of the trout was 2.4 (17). If we take the interval from fertilization to hatching in a fish as corresponding morphologically to the first five days of chick development (11) then the high R.Q.'s just mentioned would be ended, and the fat level established, in less than a chick day. In the chick itself the period of carbohydrate combustion actually occupies seven days (13, p. 993; 14, p. 592). There is evidently a fundamental difference in the utilization of energy sources between the teleost and chick egg.

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THE EFFECTS OF VARIATIONS IN ATMOSPHERIC PRESSURE UPON INSECTS[1]

By W. G. Wellington[2]

Abstract

This paper constitutes a review and an analysis of the available literature on the effects of pressure changes upon insects. The variations of atmospheric pressure that occur are classified briefly, but the effects of pressure changes upon insects are considered from the standpoint of the reactions of insects to extremely low pressure, extremely high pressure, and slight variations in pressure. It is concluded that extreme changes of pressure exert no direct influence upon insects. On the other hand, there is evidence that slightly reduced pressure increases the rates of the development and of the various activities of insects, while slightly increased pressure does not appear to have any positive influence on these processes. A discussion of the possible role of chordotonal organs in the observed responses of some insects to fluctuating pressure is included, and some laboratory experiments are suggested that might aid in quantitative determinations of the effects of varying atmospheric pressure upon insects.

Introduction

Statements have been made to the effect that atmospheric pressure must exert some influence upon various phases of insect life. However, an examination of the literature on insect ecology reveals that the effects of pressure are usually neglected. Furthermore, a more thorough search through this literature shows that the comparatively few workers who have attempted to determine the influence of pressure upon insects have produced a collection of contradictory observations and hypotheses. It is the purpose of this paper to attempt an analysis of some of these reports, in order to provide a foundation for more fruitful work than that which has been produced in the past.

Classification of Pressure Variations

Any effect that atmospheric pressure *per se* exerts upon a phase of insect life at the surface of the earth is produced by variations in the pressure. Therefore, it is necessary to have some idea of the different ways in which the fluctuations of pressure occur. It is also necessary to consider the proper units for the measurement of atmospheric pressure.

Atmospheric pressure is defined as the *force* exerted per unit area by the total column of air above the level considered. Therefore, the units of length that formerly were used for the measurement of pressure have been discarded. It has become a standard meteorological practice to express measurements of atmospheric pressure in terms of the c.g.s. unit, the *millibar*, where 1 mb. = 1000 dynes per sq. cm. Hence, for the sake of uniformity, entomologists engaged in analyses of the effects of pressure upon insects henceforth should

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adopt the current practice and express all quantitative data in millibars. For conversion purposes, 1 mb. = 0.0295 in. = 0.75 mm. of mercury.

Variations in atmospheric pressure may be classified on a temporal basis as rhythmic, irregular, or seasonal, and on a spatial basis as vertical or horizontal. Conditions under which these variations are encountered are discussed below.

Rhythmic Variations.—It has long been known that there are more or less regular daily variations in the surface pressure. Because of the complicating effects of storms in the Temperate Zones, it is often impossible to detect these small variations in any short-term barometric records taken there, since the total rhythmic fluctuations may not amount to more than 2 mb. However, harmonic analyses of long-term barometric records for such areas show 12-hr. cyclic changes culminating in maxima at approximately 10:00 A.M. and P.M., and in minima at approximately 4:00 A.M. and P.M. Near the equator, it is possible to observe these rhythms by inspection of a record, since complicating factors are usually absent at very low latitudes. Except in such tropical regions, it seems unlikely that any correlation between such barometric cycles and insect activities may be detected.

Irregular Variations.—Superimposed upon the small cyclic changes in pressure are greater changes brought about by the approach and withdrawal of migratory cyclonic and anticyclonic systems. Strictly speaking, these latter changes are not always wholly diurnal, for they are extremely variable not only in their magnitude and rapidity, but also in their times of occurrence. In magnitude, the variations may range from an over-all fluctuation of 1 to 2 mb. to one of 50 mb., and they are usually great enough to mask effectively the true diurnal pressure cycle. The rapidity of the changes may range from a total time interval of a few hours for a considerable fall and rise of pressure to one of two or three days for a more moderate fall or rise. The passage of such pressure systems over a given surface area seems to provide the most important means by which pressure variations affect insects, both directly and indirectly.

Seasonal Variations.—The atmosphere expands and becomes more humid over a warming region, while it contracts and becomes drier over a cooling region. Hence, over land masses in general, the sea-level pressure is greater during winter than in summer. With the knowledge of the effects of pressure upon insects at its present imperfect state, it is impossible to surmise how such seasonal pressure changes may affect insects directly, if at all.

Vertical Variations.—Atmospheric pressure decreases with increasing altitude. In the lowest 1000 ft. of the atmosphere, the decrease in pressure with height may be considered equivalent to a drop of 1 mb. per 30-ft. ascent. At higher levels, where the air is less dense, a millibar decrease becomes equivalent to progressively greater height intervals. If certain winged insects respond to a slight decrease in pressure, as they actually seem to do, the vertical variation of pressure may prove to be of some significance in the aerial distribution of insects.

Horizontal Variations.—The vertical variation of pressure is about 10,000 times as great as the surface variation in the horizontal direction. It is interesting to note that this slow rate of horizontal change makes pressure the *only* factor of the physical environmental complex that may be taken from standard weather station data and applied more or less directly to the microclimates of nearby areas. As long as an altitude correction is applied, this transfer of data may be carried out without endangering the validity of the actual microclimatic data. This fact provides a good reason for the entomological adoption of the millibar.

The Effects of Pressure Variations upon Insects

It has been thought that either increases or decreases in atmospheric pressure affect insects directly by influencing their rate of development; the time of their ecdysis or emergence; their feeding; oviposition; general locomotor and flight activity, and hence, their periods of activity or the times of their sporadic migrations. While there are some workers who agree that pressure does affect these phases of insect life, there is complete lack of agreement among these workers as to whether decreased or increased pressure exerts the positive influence. In the following discussion, it will be convenient to group these various problems under the broader headings that appear below.

Extremely Low Pressures

The earliest observations on the effects of reduced pressure upon insects were those of Sir Robert Boyle (3), who found that some caterpillars could survive a vacuum, while certain adult insects, such as flesh flies, could not. Huber (25) investigated the ability of bees to survive low pressure, and proved that air was necessary for life, but that the bees actually could withstand very low pressures. Bert (2) published a comprehensive work on the effects of both high and low pressures upon the life processes of plants and animals, but insects were scarcely mentioned.

A different approach to the subject was taken by Herrera and Lope (24). They reported some experiments that showed that organisms collected at different altitudes were able to survive under experimental pressures equivalent to these altitudes, as might be indeed expected.

Greenwood (21) showed that the appearance of nitrogen bubbles in vertebrate blood at very low pressure was a phenomenon that could not occur in the blood of insects under comparable conditions. Thus, it was concluded that the ability of insects to withstand extreme pressure changes is due to their tracheal mode of respiration.

In this connection, it might be mentioned that, while insects can withstand rapid decompression, certain species are temporarily affected by an equally rapid return to normal sea-level pressure. For instance, Wellington (69) observed that calliphorid flies reacted to the returned pressure by buzzing violently for a few seconds, then becoming insensible for about 15 min. It

may be concluded that these reactions result from the rapid re-inflation of the extensive air sacs of the flies, with the mechanical pressure of these on some nearby nerve centre producing temporary coma. However, on the recovery of the flies, there are no observable after-effects.

Cole (8) held 10 weevils at a pressure of 33.8 mb., and found that five still survived on the 15th day. Despite this indication that a high vacuum had no effect upon insects, other workers began to experiment with vacuum for control purposes, chiefly because the low pressure facilitated penetration of a fumigant into infested stored-products materials. Vacuum-fumigation experiments have contributed to the clarification of the actual role of extremely low pressure in the complex of factors acting upon insects under such conditions. Hence, a more detailed treatment of the results of such experiments is necessary.

Back and Cotton (1) found that insects were capable of withstanding an almost complete vacuum, and the deaths that did occur seemed to be due to an increase in the rate of evaporation and to a lack of oxygen, rather than to reduced pressure *per se*. In later papers, this hypothesis has been stated more precisely.

Cotton (10) has shown that factors affecting the susceptibility of insects to fumigants at low pressures are, respectively, increased temperature, increased carbon dioxide tension, and decreased oxygen—in short, any factor that produces an increased respiratory rate, and so results in a greater intake of toxic gas. Later, Cotton *et al.* (11) dealt solely with the effect of oxygen upon the susceptibility of insects to fumigants. They showed that, at a pressure of 84.7 mb., there was no kill by toxic gas in an atmosphere of pure oxygen, whereas a high percentage kill was obtained with the fumigant when the oxygen concentration was only 1.77%. These results confirm the view that any factor increasing the respiratory rate will increase the susceptibility of insects to toxic gases. However, in combination with the preceding results, they also indicate that greatly reduced pressure affects insects only in so far as it reduces the amount of available oxygen. This will be discussed later.

There have been some attempts to show that pressure alone affects the susceptibility of insects to fumigants. Thus, Moore and Carpenter (40) state that the percentage kill by hydrogen cyanide increases with decreasing pressure. Peters (42, 43) states that the biological effect of vacuum fumigation is due to the combined action of a reduction in pressure and a reduction in the amount of available oxygen. However, this implication that pressure plays a direct part in increasing the susceptibility seems incorrect, in view of the results of Cotton (10) and Cole (8).

The experiments upon the efficiency of vacuum fumigation have shown that a very low pressure affects the survival of insects only indirectly by reducing the amount of available oxygen below the minimum requirements for an extended period. However, since the experiments are relatively

specialized, they have not demonstrated the part played by evaporation in any deaths at low pressure.

Mellanby (36) has discussed the means by which water is lost by insects, and has shown that, at ordinary temperatures, evaporation takes place mainly through the spiracles. Thus, anything tending to keep the spiracles open, such as oxygen deficiency, provides for increased evaporation, provided that a hygric gradient exists. Obviously, low pressure will increase the evaporation from insects, and this has been shown by Livingstone and Reed (31). They found that insects survive much longer in moist air at extremely low pressures than they do in dry air at the same pressures.

It may be concluded that extremely low pressure has only an indirectly adverse effect upon insects, with the consequent reduction of oxygen and the increased rate of evaporation playing roles of almost equal importance as the *directly* lethal factors. With insects that ordinarily close their spiracles in dry air at normal pressure, the increased respiratory rate induced by oxygen-deficient air at low pressure results in a more rapid rate of evaporation through the opened spiracles. Insects that lack a closing mechanism for the spiracles will be subjected to increased evaporation at low pressure from the beginning. However, it does not necessarily follow that evaporation plays the most important part in hastening death under the unnatural conditions of extremely low pressure, since the time at which the fatal limit of desiccation is reached will be partly dependent upon the initial amount of free water contained within the insect. Consequently, it must be assumed that any mortality at a greatly reduced pressure is due to the effects of oxygen starvation combined with the effects of desiccation, and is not directly referable to the action of low pressure alone.

A few other observations, which are in substantial agreement with the preceding ones, have been made upon the effects of low pressure. Thus, Lutz (32, 33) subjected various insects to rapid decompressions and returns to normal pressure, and, as usual, found no lethal or sterilizing effects. Jollos (27) has reported sterility in *Drosophila* cultures on a mountaintop, but has made no claim that this sterility was caused by an action of low pressure.

Wellington (69) carried out a series of experiments to determine the effects of upper air conditions upon insects, and found no truly harmful effects of pressure. Woodworth (75, 76) has studied the respiratory changes in the honeybee produced by a wide range of pressures, but his work will be discussed in a later part of this paper.

The only attempt to determine whether low pressure modifies the structure of an insect is that of Margolis (35). An attempt was made to determine whether reduced pressure applied for variable periods during development would produce a change in the facet number of *Drosophila*. A slight difference was found, but it was considered to be insignificant.

Extremely High Pressures

Very few experiments have been performed to determine the effects of compression on insects. Cattell (5) has produced the most recent review on the physiological effects of pressure *sensu stricto* upon animal tissues, but has not considered insects.

Rollat (50) obtained no definitely positive or negative results when he subjected silkworm eggs to a compression amounting to three to four atmospheres. Henneguy (23) reported on much the same type of experiment, but noted that a pressure of five to six atmospheres seemed to delay larval eclosion from the eggs.

Roller (51) tested the respiratory responses of grasshoppers to increased pressure, and found that a pressure of 250 lb. per sq. in. had to be applied to abolish the respiratory movements and to stop breathing.

Cleveland (6) killed the protozoan symbionts of insects by raising the oxygen pressure. An oxygen pressure that was lethal to the protozoa left the insects unharmed. It was shown that the effects of five atmospheres of air pressure were the same as the effects of one atmosphere of pure oxygen. This demonstrated that insects can withstand a pressure of five atmospheres.

Some insects actually do experience greatly increased pressures under natural conditions. For instance, the larvae of several species of Chironomidae inhabit the benthic zone of first-order lakes. Under a water surface, an increase in depth of approximately 34 ft. increases the pressure by one atmosphere. Although this pressure is exerted by water and not by air, presumably a close analogy exists between the effects of the two types of pressure. Several workers have studied the effects of depth upon such chironomid larvae, but have been interested primarily (i.e. Cole (7)) in the adaptations of the larvae to oxygen-deficient water.

Roller's work (51) indicates that the strictly mechanical effect of great compression will stop respiration in terrestrial insects. However, it is questionable whether any resultant mortality should therefore be referable to the direct action of pressure. Undoubtedly, the actual cause of death under such unnatural conditions would be ultimate oxygen starvation, accelerated by an increased carbon dioxide concentration.

Slight Pressure Variations

The work reported in the two preceding sections makes it clear that insects are capable of withstanding extremes of pressure. Furthermore, it is clear that any mortalities that occur under these conditions are not the result of pressure *per se*. It is quite possible that such work has provided one major reason for the neglect that the study of the effects of slight pressure variations has received.

It is only logical to suppose that a factor that is harmless at a high intensity cannot have any significant effect upon insects within its normal surface range of variation. Moreover, it is equally permissible to assume that any

supposed effect of a slight variation in pressure actually would be the result of a slight change in oxygen concentration, or of a change in the rate of evaporation, just as at more extreme pressures. However, it is difficult to see how an exceedingly minute change in the oxygen concentration of the surface air can affect the metabolism of tracheate animals enough to produce the observable change in activity that occurs in insects subjected to slight pressure variations. In addition, these observable changes in activity occur through ranges of temperature and humidity wide enough to suggest that pressure alone is producing them. Hence, the effects of slight variations in pressure cannot be lightly dismissed.

The following discussion presents the conclusions drawn from various field observations, and it, in turn, is followed by a discussion of the few available laboratory observations upon the effects of changing surface pressure on insects.

FIELD OBSERVATIONS

There is no general agreement upon what type of pressure change, if any, produces reactions in insects. Some believe that low pressure increases the rates of the various activities, while others hold that high pressure increases these rates. It seems noteworthy that apparently no one has seriously considered the possibility that pressure *changes* alone might affect insects, irrespective of the direction of the changes. Finally, it is obvious from the small number of published observations that many workers feel that surface pressures have no important direct effects upon insect life, or that such effects are insignificant when compared with the effects of temperature and evaporation.

Low Pressure

Many European collectors of Lepidoptera have noted that moths may be collected in greater numbers before thunderstorms. However, whether this increase in numbers is a direct result of falling pressure has been questioned.

Sajo (52) drew attention to the fact that insects seemed to be unusually active during periods of barometric depression. Lehmann and Vaney (29) noted variations in the activity of *Hypoderma* that, on the basis of more recent evidence, might be attributed to the effects of low pressure. Marchal (34) collected a good deal of evidence to show that the electrical state of the atmosphere influenced the flight activity of vine moths. However, since the moths were more active before thunderstorms, it is possible that pressure influenced their activity.

Pictet (47) noted that Lepidoptera tend to emerge from the pupal stage during a period of falling pressure. He connected the emergence of considerable numbers of insects with a sudden drop in pressure, of perhaps only 1.3 mb., even after a long-continued rise. It was suggested that the insects required a decrease in the external pressure to enable them to break through the pupal skins.

Williams (72) noted that the waves of *Schistocerca migratoria* Forsk., which entered Egypt during the 1915 locust invasion, were all preceded by barometric depressions. This suggests that the locusts were stimulated to flight by the passage of a low pressure area, and remained active in the pressure pattern following it. Williams (72) also noted that the butterfly, *Vanessa cardui* L., has been known to follow areas of depression during migration. In addition, Steinberg (54) stated that the migrations of the sugar-beet webworm, *Loxostege sticticalis* L., are always connected with the movements of cyclonic areas.

Steinberg (54) considered that migrating webworm moths were swept towards the centre of a given low. This idea has been put forward in much the same way by Felt (18), who believed that the winds blowing towards the centre of low pressure would make a lowering pressure indirectly responsible for the drift of insects towards the centre of the low.

It should be pointed out that the anticlockwise wind systems of a low pressure area move more or less *around* the centre, and the air currents starting from a given point, either at the surface or aloft, must reach the centre only by a very devious route. A glance at a vertical cross-sectional diagram of the wind systems, frontal weather systems, isotherms, and isobars connected with a migratory, temperate-zone cyclonic area shows that an arbitrary statement concerning the ultimate distribution of drifted insects is impossible. However, the interference of the frontal surfaces with wind directions aloft (wind shear), and the interference of frontal cloud and temperature systems with turbulence and convection make it improbable that there will be any collection of insects at the centre of the low, as in the centre of a whirling vortex. To work out the probable path of actively or passively dispersed insects under cyclonic conditions, it is necessary to consider the area of low pressure by sections, and this has not yet been done.

Some workers might consider that the trapping records of Dirks (12) and of Milne and Milne (38 and 39) provide indirect evidence that low pressure activates nocturnal insects. These records show that the most favourable collecting nights at light-traps were those that were relatively warm, cloudy, and often rainy, with little or no wind. Such weather is often associated with the approach of a warm front, with a resulting drop in pressure.

Glick (20) has made extensive aircraft collections of insects in the upper air. He found an apparent correlation between the numbers of insects taken in the terrestrial zone and the actual surface pressure. The normal pressure for the area varied between about 1017 and 1022 mb. The greatest numbers of insects were taken at 200 ft. when the surface pressure was 1011.8 mb., and, from this value to 1018.6 mb., there was a gradual decrease in numbers. At pressures above 1018.6 mb., the numbers of insects taken fell off rapidly.

In addition to the above phenomenon, it was noticed that twice as many insects were taken in the low range of pressure (up to about 1013 mb.) as were collected during periods when the pressure was high (1028 to 1030 mb.) It is interesting to note that the Diptera, Coleoptera, and Hymenoptera, which possess the most highly developed nervous systems, were taken in the

largest numbers when the pressure fell slightly *below* the average value, and decreased markedly in numbers at higher pressures.

Underhill (63, 64) has found that simuliids are more active and feed more readily in regions of low or rapidly falling pressure than they do in regions of high pressure. These conclusions were made after the data had been corrected for the effects of temperature and humidity. In general, it seems to be a matter of common observation that various blood-sucking or biting Diptera are more troublesome during weather associated with a low pressure area (cf. Glick (20), Urquhart (65)).

High Pressure

Some observers believe that low pressure suppresses insect activity, and that insects are more active in high pressure areas. Thus, some say that the evening swarming of some insects follows the usual slight increase in pressure above the afternoon minimum (cf. Section II). However, Uvarov (66) has pointed out that it is more likely that this swarming is related to a definite light intensity, rather than to a definite pressure change. Indeed, the activity *rhythms* of insects often seem to be independent of any single factor.

In an oft-cited paper, Parman (41) said that adult insects seem to emerge during periods of high pressure (but cf. Pictet (47)), and found indications that nocturnal insects were more plentiful and active during times of high pressure. This seemed to be the case particularly when the barometer was rising. He also observed that migrations of *Libythea bachmanni* Kirt. took place after storms, which indicated that the flights were made during periods of rising pressure (cf. Williams (72), Steinberg (54)).

Parman (41) also reported observations made on the numbers of muscoid Diptera before and after a severe convective storm. These observations showed that the flies were more abundant before the storm than after its passage. This was attributed to the lethal effect of low pressure, but the soundness of this reasoning has been questioned by Uvarov (66) and Wellington (69). Other explanations have been offered to account for the disappearance of the insects (Wellington (69)).

Worthley (77) made a short study of the flight activity of codling moths, and found that cloudy weather retarded flight, while a slight rain stopped it (cf. Dirks (12)). Also, it was stated that a greater catch was obtained at a high pressure than at a low pressure.

Williams (74) has published a lengthy analysis of the effects of weather conditions on insect activity, as indicated by light-trap collections over a four year period. His results for pressure, corrected for the effects of wind and minimum temperature, showed that poor catches were obtained when the barometer was low, irrespective of its direction of motion, or when the barometer was high, but falling. Above-normal catches were obtained with a high barometer that was steady or rising, and with a medium (normal) barometer.

Ordinarily, one would be inclined to accept the conclusions indicated by this analysis solely on the basis of the huge quantities of material available

for treatment. However, closer inspection indicates that the necessary simplification of the data prior to statistical treatment has resulted in the omission of an important point. For instance, the light-trap used was so compartmented that it divided each nightly catch into eight separate collections (Williams (73)). This, of course, is a highly desirable feature, for, with such a mechanism, it should be possible to make a direct comparison between the numbers of insects in each of the eight collections and the amounts and directions of the pressure changes before, during, and after each collection. However, for the actual statistical treatment (74), the midnight barograph reading was taken as the pressure measurement for the night.

It is difficult to see just how one can determine whether the pressure is falling, rising, or steady, if a single reading is taken as being representative for the whole night. Moreover, such over-simplification completely discards any real correlation between the activity of the insects during the eight periods and the pressure changes during those periods. Unless the data are treated in a different manner, it is impossible to consider the results as significant.

In closing this section on field observations, it should be noted that some workers have found no significant correlation between the fluctuations of pressure and any particular phase of insect life. Thus, Cook (9) felt that pressure exerted an insignificant amount of influence upon insects compared to temperature or humidity. Similarly, Sweetman (61) concluded that pressure was of no significance in the physical ecology of *Phyllophaga* sp. Speyer (53) found no noticeable effect of pressure upon the adult emergence of *Cheimatobia brumata* L., while Stirrett (56–60) concluded that pressure had no effect upon the flight activity of *Pyrausta nubilalis* Hbn.

Obviously, there are many times when any direct effect of pressure upon insect activity will be overshadowed or completely nullified by the direct effects of temperature or evaporation. Thus, Stirrett (56–60) found that the corn borer moths flew immediately after one thunderstorm, but did not fly for two hours after another storm. This might have been taken as an indication of a response to increased pressure by either of the two preceding schools of thought. However, this instance actually serves to draw attention to the fact that pressure may indeed be overshadowed by other factors, particularly after the passage of thunderstorms.

Any consideration of the effects of thunderstorm passage upon insects should take into account the fact that different types of thunderstorms leave very different conditions of temperature and humidity in their wakes. Thus, air-mass storms, produced by instability within the air mass, often leave temperature and humidity conditions little changed behind the immediate storm area. On the other hand, frontal thunderstorms presage relatively great changes in the above conditions, leaving either warm and moist, or cold and relatively dry conditions in their wakes, depending on whether the front is warm or cold. Consequently, it is important to distinguish between these types of storms before drawing any conclusions concerning the relative importance of any direct effects of pressure on insects after a given thunderstorm.

LABORATORY OBSERVATIONS

It is obvious from the conflicting points of view that are presented above that there is considerable disagreement concerning the effects of pressure upon any phase of insect life. It is equally obvious that any solution of the problem must depend first upon the laboratory, where *all* factors may be closely controlled.

Pictet (44–46, 48) conducted rearing experiments to determine the effects of different pressures upon the development of Lepidoptera. It was found that a uniform pressure prolongs the pupal stage, and, significantly, that either a uniform pressure or a slight *rise* in pressure just prior to the emergence of an adult might delay such emergence until the insect dies within the chrysalis. On the other hand, *reduction* of the pressure during the whole pupal period shortens this stage considerably. Thus, at pressures of approximately 946 to 970 mb., the pupal stage of *Pieris rapae* L. was shortened from 15 days to 9 days. As noted previously (Pictet (47)), it was also found that a drop of about 1 mb. just prior to the calculated time of emergence hastened that act.

It is regrettable that this type of work has not been carried on by others, and that no one has timed the developmental rate at pressures slightly higher than normal sea-level pressure. Margolis (35) missed an opportunity to record some useful information on developmental rate at low pressure by becoming too concerned with the facet number of *Drosophila*.

Woodworth (75, 76) has investigated the effect of reduced pressure on honeybee respiration. This was done over a wide range of pressure (932 to 66 mb.), but his results are more properly included in a discussion of the effects of slightly or moderately reduced pressure. It was found that the oxygen consumption of the bees increased as the pressure fell from about 800 mb., reaching a peak at a pressure of about 650 mb. With further reductions of pressure, the oxygen consumption fell almost logarithmically from its peak to a subnormal rate at a pressure of 220 mb.

The sudden rise in respiratory rate noted above is interesting in view of Glick's (20) aircraft collections and the pressure experiments of Wellington (69). In the latter experiments, it was found that Diptera, and muscoid Diptera in particular, showed markedly increased flight activity as the pressure fell from its normal value. Maximum activity was observed at about 890 mb. It has been pointed out (Wellington (68, 69)) that the observed activity range corresponds remarkably well with the altitudes of maximum concentration of these insects in the atmosphere as determined by Glick (20). Unfortunately, Wellington did not test any Hymenoptera in these pressure experiments, and Woodworth (75, 76) made no comment on the locomotor activity of the bees during his experiments.

Woodworth (76) termed the initial increase in respiratory rate "compensatory metabolism", and considered that it later wears off to reveal the depressing effect of greatly reduced pressure (i.e.—lack of oxygen). However, at a *slightly* reduced pressure, it is quite possible that such an increase in

respiratory rate might be the direct result of increased activity. In this case, if the pressure reduction is slight, so that there is no danger of an overlapping of the effects of oxygen starvation plus desiccation with any effect of pressure *per se* upon activity, such "compensatory" metabolism should persist throughout the duration of the induced activity.

No one has ever made any observations to prove or disprove the above statement. However, Wellington (69) attempted to determine whether the increased activity observed in Diptera was the result of slightly reduced air pressure, oxygen tension, or carbon dioxide tension. In this experiment, activity was produced in the flies by lowering the pressure, and then nitrogen was passed into the bell-jar to raise the air pressure to its initial value. This procedure left the oxygen–carbon-dioxide tensions at the "low pressure" values. Therefore, if these tensions had directly affected the activity, such effects should have persisted when the *air* pressure was raised. However, since the activity of the flies dropped back to normal at the normal pressure, it was concluded that the initial increase in activity observed was caused by the lowered pressure alone. It should be noted that this experiment did not take into account any changes in the rate of evaporation at the two pressures.

The activity observed in Diptera at reduced pressures has been termed "barotaxis" (Wellington (68, 69)). However, further investigations (Wellington (71)) have shown that two types of activity can be distinguished in the responses of muscoid Diptera to fluctuating pressure, and it seems likely that this distinction may soon be extended to the reactions of many other dipterous insects to pressure changes.

There is a directed response (a true taxis) to slight, extremely localized increases in pressure, or pressure waves, such as those started by hand motions. The flies react baronegatively to such waves even after the visual component is removed. This reaction is dependent upon the vibrations of the aristae and certain other antennal structures, which act as baroreceptors.

The second type of activity that may be distinguished in the flies is that type that was initially observed (Wellington (69)) and misnamed "barotaxis". This response to even very slightly reduced pressure is completely undirected, and takes the form of a general increase in locomotor activity, which ceases when the pressure is returned to normal. This type of activity has been called a kinesis (Wellington (71)). The important distinguishing feature of the kinetic type of activity is that it is exhibited both by flies possessing functional baroreceptors and by flies *lacking* baroreceptors.

It has been shown (Wellington (71)) that a combination of the barokinetic response to decreased pressure and the tactic response to localized pressure waves provides a good explanation for the typically nervous activity exhibited by muscoid Diptera before thunderstorms. Such activity has been noticed and discussed by Parman (41), Sterzinger (55), and Wellington (69, 70). Wellington (71) considers that slight, intensely localized increases in pressure superimposed upon the falling pressure ahead of a thunderstorm are more

than ample to stimulate the flies by vibrating the antennal baroreceptors. The typically erratic flights are produced in this way.

The latter hypothesis not only suggests the true mechanism of the reaction of muscoid Diptera to thunderstorm pressure patterns, but also suggests that comparable activity should be induced in any insects possessing well-developed, complex chordotonal organs (e.g.—many male nematoceran Diptera, or acridid Orthoptera). Any sensory apparatus capable of receiving sonic vibrations should be stimulated to a lesser extent by grosser pressure vibrations in the atmosphere.

It is interesting to find that Vayssière (67) suggested that migratory locusts are stimulated to flight by the aerial vibrations given off by the flight movements of other locusts passing overhead. De Lepïney (30) has carried this further, and has found that blinded locusts will still respond to the passage of a flying locust, but that locusts enclosed in glass will *not* respond. Furthermore, Ramchandra Rao (49) noticed that locust bands became inordinately active before a thunderstorm. If individuals were caged, they still responded to the approaching storm by exhibiting marked restlessness. It is possible that these observations contain the key to the explanation of the marked association of locust swarms with migratory storm centres that has been noted by Williams (72) and others.

Conclusions

Effects of Extreme Pressure Changes

It is certain that neither extremely low nor extremely high pressures produce any adverse physiological changes in insects that can be directly attributed to the effects of pressure *per se*. Any adverse results of such exposures must be attributed to the effects of oxygen starvation plus or minus a changed rate of evaporation.

Effects of Slight Pressure Changes

The reactions of insects to slight changes of pressure suggest that changes in insect metabolism are produced by the effects of pressure alone. The activity induced by slight pressure reductions must be completely independent of any minute change in oxygen concentration produced by a surface pressure change. Furthermore, there is evidence that suggests that such increased activity produces an increased respiratory rate, although the reverse is not necessarily true. Finally, there is enough variation in atmospheric humidity and temperature when such changes in activity (and pressure) take place to indicate that the change in activity is dependent solely upon the pressure change.

EFFECTS OF SLIGHTLY REDUCED PRESSURE

All the laboratory evidence, and the majority of the field evidence indicates that any observable increase in insect activity that may be attributed to pressure is produced only by slightly lowered or falling pressures. However, at the present time, it is necessary to limit such activity to the undirected,

or kinetic type, if *low* pressure alone is stipulated as the causative agent. This will be discussed later.

EFFECTS OF SLIGHTLY INCREASED PRESSURE

There is no trustworthy evidence to indicate that high pressure stimulates insects to greater activity. The views of authors who differ from this opinion are based chiefly on rather casual observations.

It has been stated that migrations of insects take place after the passage of a low, and hence occur in the region of rising pressure. However, it is admitted that the insects appear progressively behind the receding low. If such a migration is in response to *increasing* pressure, the direction of flight should be directly towards the centre of the oncoming high, since the pressure is highest there. Since this does not occur, it must be concluded that such insects are activated by some factor associated with a low pressure area that is absent from a high pressure area. This factor, in some cases, seems to be low pressure itself. However, in a few cases, fluctuating pressure alone might produce reactions, irrespective of the direction of the pressure change. This is discussed more fully below.

EFFECTS OF SLIGHT FLUCTUATIONS OF PRESSURE

Lowered pressure acts to increase the rates of various activities of insects, including undirected locomotor activity. However, since this locomotor activity, including flight activity, is undirected, the question naturally arises why some migrating butterflies, locusts, etc., follow moving low pressure areas. Their actions imply a directional element in response to lowered pressure, which no experiments have yet shown to exist.

In the case of migrating rhopaloceran Lepidoptera, lacking tympanal organs, there is no completely satisfactory explanation for this phenomenon at the present time. It is possible to assume that the migration, once started by lowered pressure, stays within the zone of stimulation, and this may yet prove to be true. However, until more exact data are obtained that show the actual positions of the migrants in relation to the warm- and cold-frontal regions of a depression, this must be considered to be an extremely tentative explanation.

In the case of migrating locusts, which possess tympanal organs, a more satisfactory explanation may be put forward. It is possible that their flight activity is intimately linked with the fluctuations of pressure common in the immediate vicinity of the cold-frontal zone, which brings up the rear of a depression. In other words, it is possible that the position of the locust bands is due to the fact that they are kept stimulated to flight by the vibrations set up by the myriad localized pressure changes associated with the unstable conditions that characterize the cold-frontal zone of a depression. It is impossible to say whether barokinesis in response to low pressure plays any part in such a reaction, as it does in the case of muscoid Diptera. However, once started in flight by pressure fluctuations alone, the locusts would continue

to be stimulated by such vibrations and by each other. Their flight might keep them within the zone of stimulation until they were forced to drop to the ground by temperature changes or by other changing physical or biotic factors.

Basis of the Reactions of Insects to Pressure Changes

Pressure fluctuations seem to produce changes in locomotor activity in those insects that possess sensory structures capable of receiving auditory stimuli. For instance, muscoid Diptera react to localized increases in pressure that affect the position of the aristae and Johnston's organs (although, in this case, these structures may have no truly auditory function). Saltatorial Orthoptera and many heteroceran Lepidoptera, all possessing tympanal organs, may react to localized fluctuations of pressure. (For a discussion of the structure and auditory function of the tympanal organs of Lepidoptera, *vide* Eggers (14, 15, 16, 17) and von Kennel and Eggers (28).) Such reactions, which are or may prove to be of a directed nature, are dependent upon the possession of specialized sense organs that may be primarily or secondarily baroreceptive in function.

However, the increased rates of development, locomotor activity and feeding activity, and the sudden occurrence of mass emergences that occur at slightly reduced pressures are not easily linked to any supposed stimulation of special sense organs. Indeed, specialized organs of the tympanal type may be entirely lacking, as in rhopaloceran Lepidoptera, or the general increase in the rates of various activities may be independent of the presence of proved baroreceptors, as in muscoid Diptera. Hence, all that may be said at present is that slightly reduced pressure seems to increase the rate of development and of energy expenditure of higher insects, but no highly specialized sense organs seem to be required for this general stimulation. Further speculation would be unproductive.

Relative Importance of the Effects of Pressure

In closing this section, it is necessary to point out that the effects of pressure changes upon insect life may be obscured or completely nullified by changes in temperature or evaporation. However, it does not follow that pressure is a factor that may be ignored in insect ecology. Insects are active within relatively wide ranges of temperature and moisture conditions, and, in many cases, it is necessary for one or both of these factors to change by a considerable amount before any noticeable effect on insect activity is produced. Insects also are active over extremely wide ranges of pressure, but, within the surface range, a surprisingly slight change of pressure produces a noticeable effect upon insect activity. The practical applications of this fact in chemical and natural control, and in preventive entomology should not be overlooked, particularly when it is realized that it is often far easier to forecast a change in pressure than it is to forecast the weather accompanying the change. Thus, it is obvious that more exact studies on the effects of pressure upon insects should produce valuable results.

Appendix

Suggestions for Future Research

This paper, with its numerous hypotheses, has shown how little actually is known about the true effects of atmospheric pressure upon phases of insect life. It is evident from the preceding discussion that the primary and most difficult goal for future workers in the field is the final solution of the underlying physiology of the effects of slight variations in atmospheric pressure upon insects. Delay in the solution of this problem need not prevent the beginning of more exact work on easier problems in the general field. Consequently, suggestions for the beginning of a few of these problems are added below.

More exact laboratory work is needed, particularly in the case of the effects of pressure on locomotor activity. The few experiments on this cited in this paper must be put on a quantitative basis. Present-day laboratories are equipped with rooms or incubators in which all physical factors other than pressure may be closely controlled, and many of the biotic factors may be kept relatively constant also. A barograph in the room permits evaluation of any supposed pressure effects. In addition, there are a number of common experimental insects for which the temperature, moisture, light, and food requirements are known rather exactly. With this combination of equipment and material, it should be possible to design some experiments that should produce some significant results, instead of further confusion.

There is equipment available that should aid any attempt to place the effects of pressure on locomotor activity on a quantitative basis. Syzmanski (62) designed several variations of an instrument termed the aktograph, by means of which the activity of a caged animal is traced on a revolving drum, from which it can be translated in terms of cage-length distance travelled. This apparatus gives a close evaluation of the effect of a variable factor upon the locomotor activity of an animal.

Gunn and Kennedy (22) have described adaptations of the aktograph that fit it for use with insects of cockroach size. Edney (13) used a further adaptation (actograph), which was markedly improved by making the activity cage so narrow that the enclosed insect was restricted in its movements to the long axis of the cage. Using Edney's adaptation as a basis, it should be possible to modify the apparatus for lighter insects by using a lighter pen arm, and a gauze cage, instead of a relatively solid one. The tracings made over 24-hr. periods with such an instrument should yield data of significance when compared with a barograph tracing showing the natural variations in the pressure.

Yeager and Swain (78) have described an entomograph, which measures the force in dynes exerted by an active insect, and so indicates its comparative activity. This equipment is useless for any lengthy study of pressure effects, because it restricts the movements of the insect too much, but it might prove useful in any attempt to measure the degree of activity resulting from sudden, controlled changes of pressure. In its present form, this apparatus must be used with insects of cockroach or locust size.

It is especially important to determine the effects of atmospheric pressure upon the feeding activity of Diptera attacking man and animals. If the increase in the number of attacks can be put on a quantitative basis, future attack periods should be predictable with considerable accuracy (cf. Wellington (68)). The economic importance of this is obvious, if such sudden great losses of cattle as those reported by Millar and Rempel (37) are to be prevented. Given pressure as the only variable, it should be possible to determine the readiness with which biting Diptera attack animals in the laboratory under different surface pressure conditions. Recently, Frings and Frings (19) have described an instrument for measuring the feeding rate of haustellate insects that might well be incorporated into any such experiments with some blood-feeding or ordinary Diptera.

The effects of pressure upon larval or adult emergence should be relatively easy to observe under laboratory conditions. (It is assumed that no special vacuum apparatus is available, so that the pressure varies normally in the following procedure.) To observe the effects of pressure on emergence, it is necessary to construct an apparatus that rotates at intervals, separating any emerged insects into groups according to the time of their emergence, in much the same manner that the light-traps of Williams (73) and Hutchins (26) separated trapped insects according to the time of their flight. Cagle (4) devised a compartmented disk, which was shifted by a clock, as an aid in determining the times at which oriental fruit-moth larvae left samples of fruit. A more closely compartmented apparatus, making use of the phototactic tendencies of adults and larvae should provide a very suitable approach to the problem of the effects of pressure on emergence.

The examples cited above constitute but a very few of the many problems that occur in the field of pressure studies. Other examples will readily occur to the interested reader.

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PARASITES, DISEASES, INJURIES, AND ANOMALIES OF THE COLUMBIAN BLACK-TAILED DEER, *ODOCOILEUS HEMIONUS COLUMBIANUS* (RICHARDSON), IN BRITISH COLUMBIA[1]

By Ian McTaggart Cowan[2]

Abstract

The occurrence of parasites, parasitic disease, some non-parasitic diseases, and certain anomalous conditions in the Columbian black-tailed deer, *Odocoileus hemionus columbianus* (Richardson), in southern British Columbia is outlined. The parasitological findings are in two categories: those based upon a random sample of 40 wild deer, and those based upon 25 additional deer examined in their entirety and others in part. Twenty-five species of parasites, 8 arthropods and 17 helminths, were recovered. Comparison of parasitism in young and adult deer reveals a few differences in the species of parasites present but both age groups are almost equally susceptible to arthropods and to helminths. Five species of parasites, *Cephenemyia jellisoni*, *Oesophagostomum venulosum*, *Dictyocaulus viviparus*, *Fascioloides magna*, and *Nematodirus filicollis*, were found to induce disease that was not infrequently fatal. Some evidence was secured that cursorial predators selectively remove the more heavily parasitized deer.

Ten anomalous conditions arising from non-parasitic disease, injury, or congenital deformity are described but none of these was sufficiently frequent to take an important place in the life equation of the deer. Incidence figures are given for various anomalies of form and position of the teeth and for dento-alveolar abscesses and one instance of caries and one of paradontal disease are reported.

The study did not include bacteria and viruses as agents causing disease in deer and the only pathogenic micro-organism identified was *Actinomyces israeli*.

There may be areas in which the absence of predators and of parasites permits the Columbian black-tailed or coast deer to extend its life span until loss of teeth brings death from malnutrition alone, but the existence of such is seriously doubted. The examination over the past 15 years of about seven hundred of these deer has revealed only one that exhibited a dental condition suggesting that mastication was becoming difficult as a result of the normal tooth attrition accompanying old age. This, an aged buck taken at Chemainus, V.I., B.C., on Mar. 19, 1940, was suffering also from heavy parasite infestation.

Analysis of the causes of death among coast deer indicates that disease, starvation, and predation, including that of man, are the three major factors. No deer have so far been encountered in British Columbia in which death from starvation was not complicated by, or largely the result of, heavy parasitism, and there are many indications that parasitism is frequently involved as a factor predisposing the host to selective loss through predator activity.

The study upon which this report is based was undertaken to determine the species of parasites to which the Columbian black-tailed deer is host and

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the importance of these as destructive agents; also to investigate the prevalence and importance of non-parasitic diseases, injuries, and anomalies in the species.

Data upon local epidemics and upon the occurrence of certain species of parasites have been accumulated gradually since 1927, but from 1938 to 1944, the study entered a more intensive phase and wherever conditions made such possible, a thorough examination was made of every deer taken or received.

To determine the incidence of parasitism in the normal population a random sample of 40 deer was taken at various times of the year on southern Vancouver Island. On the Goldstream watershed 19 miles northwest of Victoria, B.C., deer were collected for this purpose specifically and whenever a specimen was sought the first deer presenting itself was shot. Elsewhere the deer were obtained where they were damaging crops or where they had been accidentally killed on the highways.

It is possible that one cannot obtain a strictly unbiased sample in this way, that the more heavily parasitized deer have their senses dulled and their faculty for escape impaired, and are consequently more easily secured by the means employed. On the other hand, it has been found that injured or seriously diseased deer tend to skulk in dense thickets, and in consequence are frequently less likely to be eliminated by human agency.

Apart from bias arising from such factors, the sample obtained is believed to present a fair picture of parasitism on southern Vancouver Island, an area where predator control, involving the destruction of wolves and mountain lions, has been practised strenuously since 1922.

The random sample includes 15 does two years old or over, three yearling does, 14 bucks two years old or over, three bucks between a year and two years, and five deer less than one year old.

The population from which the sample was drawn was a sedentary one with a mean density of approximately 20 deer per square mile. Food supply was adequate.

Many additional data upon parasitized deer were obtained from 25 specimens brought to me, because they were apparently diseased, by sportsmen or by the officers of the British Columbia Game Department. These deer originated both on Vancouver Island and on the mainland and small contiguous islands adjacent to Vancouver, B.C. Data so obtained have not been used in the study of incidence in the normal population but are given separately.

No protozoan parasites of the blood stream have been detected, nor any protozoa producing lesions in the digestive tract or other organs.

The role of bacterial and virus infections has not been investigated. To date the only bacterial organism identified as a pathogen has been *Actinomyces*.

Arthropod Parasites

In determining the actual or relative abundance of external parasites, two methods were used. Ticks, which were usually confined to certain more or less limited areas of the body, and were seldom abundant, were

counted in their entirety. The same was attempted with light infestations of *Lipoptena* but the mobility of this fly renders the figures so reached less reliable.

It is not possible to count all individuals of lice, unless some method involving the dissolution of the hide and hair is employed. With these insects, computations of relative abundance were resorted to. Five pieces of hide, each 1 sq. in. in area, were removed by cutting from the skin side. These were taken in a line from the inguinal region to the mid-dorsal line over the shoulder. Counts of lice on these squares were made and a mean figure arrived at. Under circumstances that did not permit such counts, a loose classification into very heavy, heavy, moderate, or light infestation was made.

Lipoptena is too active to be counted by this method. With this species, total counts of some of the lightest infestations were made but the general procedure was merely to classify them as very heavy, heavy, moderate, or light infestations.

Winter Tick—*Dermacentor albipictus* Packard

Dermacentor albipictus was the most abundant tick encountered. It was present on 11 of the 40-deer sample as well as upon a large proportion of the other deer examined. However, as many of the deer in the sample were taken during the period when this tick is inactive, a more accurate statement of incidence is that 9 out of 17 deer, taken between Sept. 1 and Jan. 31, were infected. To date it has not been found on the mainland of British Columbia (the number of deer examined was small, however), but has been recorded at all points along the east coast of Vancouver Island from Victoria to Menzies Bay, and on Hardy Island adjacent to the mainland coast.

This tick is usually scattered widely over the body of the deer, but the greatest numbers are invariably on the back and sides of the neck and on the top of the shoulders. The feeding punctures seldom show associated inflammation and in this respect are unlike those of *Ixodes*.

The heaviest infestation noted was at Crofton, V.I., on Oct. 8, 1938. There an adult buck bore ticks estimated to number at least one per sq. in. of body surface, or a total of approximately 1200. In this infestation, larvae and nymphs predominated, the proportions being 73% seeds, 22% nymphs, 5% adults.

Though my collections of *D. albipictus* on the coast of British Columbia have not been extensive (Table I), they nonetheless serve to indicate that the life history of this species on the coast differs considerably from that of supposedly the same tick in the Rocky Mountain region. In the latter area, the larvae begin feeding with the first frosts in September and October, but the adults are not present in maximum concentrations until March and April, and persist in large numbers well into May.

On Vancouver Island the larvae begin to appear on the host in late summer and reach the highest point of their abundance in October. Hearle (11),

TABLE I

SEASONAL COLLECTIONS OF *Dermacentor albipictus* FROM DEER ON SOUTHERN VANCOUVER ISLAND

Locality	Date	Larvae	Nymphs	Adults
Goldstream Lake	Jan. 6		4	
Cowichan Lake	Jan. 31	2	2	3
Goldstream Lake	May 10			1
Cobble Hill	July 29		1	
Duncan	Sept. 29	2	1	
Crofton	Oct. 8	876*	264*	60*
Goldstream	Oct. 31		2	13
Goldstream	Nov. 1			2
Goldstream	Nov. 10	2	5	
Goldstream	Nov. 18		10	15
Campbell River	Nov. 21	2	15	47

* *Estimated from sample counts.*

referring to an unstated region, states that the seeds moult in about 10 days and that the entire feeding period from seed to engorged adult may take only six weeks. My data indicate a similar condition on Vancouver Island, where adult ticks predominate on the host by late November. Though 22 deer were examined between February and July, on only one of these was there *Dermacentor* present, one nymph on a deer from Cobble Hill on July 29.

Because this tick is present on the coast deer only in the autumn and early winter, when the deer are in good condition and food abundant, their effect upon the host is much less important than it is under the conditions prevailing in the Rocky Mountain region. There the tick may be so abundant on host animals in the winter and spring that deaths from tick poverty are common.

CALIFORNIA TICK—*Ixodes californicus* Banks

This tick is not abundant on Vancouver Island but is common on the adjoining mainland. In British Columbia it is restricted to the east coast of Vancouver Island, north to the vicinity of Comox, and to the Fraser delta and adjacent coastline north about to Jervis Inlet.

Six deer of the 40 bore one or more ticks of this species. Single individuals were taken from deer on Nov. 10, Jan. 6, Feb. 13, May 6, and July 29. Localities represented were Goldstream Lake, Brentwood, Duncan, Cobble Hill, and Cowichan Lake.

All *Ixodes* taken from deer were attached in the axilla, inguen, lower abdomen, and inside of the thigh of the host. Inflamed areas $\frac{1}{2}$ to 3 in. or more in diameter characteristically mark the site of a feeding tick. In two deer from Hardy Island, Apr. 3, 1943, each with heavy *Ixodes* infestation, the lymph glands of both axilla and inguen were hyperaemic and enlarged.

Records to date indicate a year-round activity of the adults as parasites of deer but there is a concentration of activity in the late winter and spring.

The heaviest infestation noted on Vancouver Island consisted of 23 adults of both sexes on a buck taken at Cowichan Lake on Jan. 31, 1940.

This is a three-host tick. Jellison (12) in California and Gregson (7) in British Columbia found lizards to be the main hosts of the larvae and nymphs. In British Columbia the lizard host is *Gerrhonotus principis*, the only species occurring in the coastal habitat of the tick.

Individual lizards may support large populations of young ticks. One taken at Watson Lake near Victoria on May 15, 1940, bore 79 larvae and 21 nymphs in its ears and gular folds. Lizards taken in the same area on June 30 were uninfested.

Deer Botfly—*Cephenemyia jellisoni* Townsend

This fly has a wide distribution in the range of the coast deer. It is known to occur in California as far south as this deer ranges and has been reported as a serious deer parasite in coastal British Columbia as far north as Porcher Island.

Details of the life history of this fly observed during the present study have been recorded elsewhere (3). In brief, first instar larvae, deposited in the noses of the deer during the summer and early autumn can be found crawling over the nasal mucous membranes. Shortly after moulting to the second instar they enter the retropharyngeal pouches where they remain until maturity. They then leave the host to pupate in the ground. Mature larvae reach a length of 35 mm.

Bots were present in 12 of 40 deer examined for them. Numbers per host varied from 4 to 48. Two deer containing 35 and 48 were dead or dying when discovered. In both, other parasites were scarce. Another deer, a senile buck taken at Chemainus, V.I., on Mar. 19, 1941, bore 44 *Cephenemyia* larvae and at the same time supported unusually heavy infestations of lungworm and caecal worm. It was very emaciated.

The first heavily infested animal examined was a yearling doe captured alive, but in a dying condition, at Sooke, V.I., on Mar. 20, 1938. When first discovered the animal staggered to its feet and endeavoured to escape but after a few steps fell to the ground and ceased struggling. It died during the 20-mile car journey to the laboratory.

This animal was extremely emaciated, the subcutaneous tissues between the mandibles and over the upper throat were dropsical, there was a slight mucopurulent discharge from the nostrils, and the hocks were soiled from a chronic diarrhoea. Biting lice were abundant but there were no parasites in the lungs or digestive tract except the 48 third instar *Cephenemyia* larvae in the nasopharynx. These had induced considerable local inflammation and had apparently led to secondary infection of the mucous membranes of the region. The brain was not examined but there were no other macroscopic lesions.

The second heavily infested animal was an adult doe found dead near Maple Bay, V.I., on Apr. 8, 1939. The picture was similar with a chronic dysentery, nasal discharge, and inflammatory congestion of the nasopharynx. There were some lung adhesions, the result of a previous lungworm infestation, but no other parasites of the pulmonary or digestive tracts. Thirty-five third instar larvae were still present and doubtless others had already left the animal.

While it is possible that death ensued as a result of undetermined factors, the conclusion reached was that the presence of the bots was the primary, if not the only, cause.

One deer, later found to be heavily parasitized by bots, suffered severe vomiting attacks during the early spring. These may have been induced by the movements of the mature larvae. If this is a characteristic symptom of such parasitism the debilitating effect of the bots is easily understandable.

Small haemorrhagic areas on the mucous membrane of even lightly infested retropharyngeal pouches frequently, but not always, accompanied the presence of this parasite. A heavy mucous discharge was almost universal. Infested pouches were many times normal size. Histologically the mucous membrane was necrotic with the epithelium sloughing to or below the basal layer.

There are several previous reports of deaths among deer attributed to *Cephenemyia* infestation. Bruce (1) records an epidemic of "nose fly" on Porcher Island, B.C., apparently responsible for large scale losses to the deer population. Since then a similar outbreak apparently killed the greater part of a herd of 150 semi-tame deer on Hardy Island, B.C.

Walker (25) describes the death of more than 60 deer from one herd of mule deer (*Odocoileus hemionus hemionus*) in Colorado between February and April 1929. Deer involved were mostly young animals but some adults died also. One examination revealed 54 *Cephenemyia* larvae in a dead deer that had the tissues of the lower nasal passages highly inflamed and an infection in the upper left sinus that had extended to the adjacent lobe of the brain. Deer were reported to be restless for 24 hr. prior to death and to die in apparent agony with the head drawn back toward the shoulders.

Van Roekel (24) believed that the presence of bots in California deer was partially responsible for an acute inflammatory condition of the eye accompanied by ulcerative keratitis and leading eventually to opacity of the cornea and total blindness.

There has been no indication of such sequalae in any of the cases examined during the present study.

Though experimental evidence of the effect of the *Cephenemyia* larvae upon the health of the host is lacking, there is a considerable body of circumstantial evidence to suggest that the deer bot, if present in numbers greater than 30 individuals can have serious consequences and may kill the host.

More often perhaps, the lighter infestations constitute just one link in a chain of multiple parasitism that cumulatively debilitates and frequently kills the host.

BLOWFLY—*Phormia regina* Meigen

Blowfly infestations of wounded deer are probably fairly common during the summer months, but inasmuch as wounded or diseased deer seek the seclusion of dense cover such cases are seldom encountered in the wild.

Only two such instances of myiasis have come to my attention. In July, 1936, an injured deer was discovered close to the Island Highway 12 miles west of Victoria suffering from a compound fracture of the femur as a result of a heavy blow, probably by an automobile. The wound contained large numbers of fly maggots that, upon rearing, proved to be those of *Phormia regina*.

In July, 1941, a three-legged fawn, captured and held in captivity at Cowichan Lake, died from faulty feeding complicated by myiasis of the rectum. The species of fly involved in this case was not determined.

DEER LOUSE FLY—*Lipoptena depressa* Say and *Neolipoptena ferrisi* Bequaert

Two species of louse fly occur on the coast deer in southwestern British Columbia, but inasmuch as no difference has so far been detected in their life histories as associated with the deer, they will be treated together.

Spencer (21) has discussed the distribution of the two species in western North America and finds that *Lipoptena depressa* is the predominant species on the coast deer but that *N. ferrisi* has been taken from the north end of Vancouver Island; Campbell River, V.I.; and Pemberton, B.C. Life history notes accumulated during the present study have been published elsewhere (3).

The louse fly is perhaps the most widely distributed of all parasites of the coast deer. Of 44 deer examined for its presence, only two were negative, one in December, one in January.

Infestations reached a maximum in the late summer and early autumn, at the end of the period of emergence, and gradually decreased to a minimum in May and June just prior to the emergence of the new generation of winged adults. Heaviest infestations averaged two individuals per sq. in. of body surface, which on a deer with a body area of between 1000 and 1200 sq. in. indicates a population of *Lipoptena* of between 2000 and 2400 individuals.

On several occasions the writer has found feeding punctures that he ascribed to this parasite. Each puncture was the centre of a small red spot and in some cases a small amount of dried exudate was present at the site of the puncture. Though this parasite is present in greatest numbers when the deer are at their optimum condition, nevertheless the irritation caused by the very heavy infestations must have considerable deleterious effect upon the host.

HUMAN FLEA—*Pulex irritans* Linnaeus

Deer do not normally support fleas. The only flea I have found on the coast deer crawled off a tame animal onto my hand. This deer was in a pen to which a dog had access and there is little doubt that the flea had originated on the dog and was merely an incidental parasite upon the deer.

Sucking Deer Louse—*Cervophthirius ferrisi* Mjoberg

The sucking deer louse is apparently of infrequent occurrence on the coast deer. It was recovered from two of 40 deer examined for it between 1937 and 1941. Fifteen specimens were removed from the dorsal part of the neck of a deer taken at Duncan, V.I., on May 6, 1940, and a single specimen was taken from the neck of a deer shot at Goldstream Lake, V.I., on May 21, 1940. Prior to this, Spencer (21) had recovered two of these lice from the neck of a deer shot by the author at Comox, V.I., on Nov. 12, 1930.

Biting Deer Louse—*Tricholipeurus parallelus* (Osborn) and *T. virginianus* (Peters)

Two closely allied species of biting louse have been identified from collections taken from deer on Vancouver Island, Hardy Island, and Abbotsford and Howe Sound on the mainland.

The biting louse is one of the most universally distributed of deer parasites on Vancouver Island. It was present on 29 out of 40 deer examined for it, frequently in enormous numbers.

On healthy deer the louse population becomes small during the late summer and early fall and increases steadily as the deer lose condition during the winter and spring. Ailing deer in every instance have been found to support heavy to very heavy louse infestations. As described above louse populations were estimated on a square inch basis. Table II outlines the results of examinations made upon the random sample of deer from southern Vancouver Island. Where lice were scarce they tended to be distributed on the abdomen and on the neck, with eggs most abundant on the neck. In heavy infestations on the other hand, adults, juvenile stages, and eggs were fairly evenly distributed over all the long-haired parts of the body. If the surface area of a small deer be taken as approximately 1000 sq. in. it will readily be appreciated that enormous numbers of lice are represented in an infestation averaging 140 per sq. in. Under such conditions individual hairs may support four or more lice. A maximum population of this density was found on two deer, both yearlings in very poor condition.

The irritation caused by infestations of such magnitude must be intense and doubtless contributes in no small part to the poor condition of the host. All the deer having very heavy infestations of lice were at the same time host to the heaviest infestations of caecal worm (*Oesophagostomum*) encountered and possibly the presence of these worms had so reduced the resistance of the deer that louse populations were able to pyramid.

In such acute phthiriasis there is pronounced pruritus of the skin; the pelage is rough and unthrifty, often patchy; the deer manifest the irritation by biting themselves frequently and scratching with the hind hoofs. On infrequent occasions I have observed an animal rubbing itself against a stone or other object but this action is not characteristic.

Little is known concerning the mechanism whereby a host controls the numbers of its parasites. A significant possibility is suggested by the findings of Kartman (14) that the feeding of a diet high in vitamins A and B_2 enabled rats to rid themselves of lice. The winter diet of the coast deer in this area may be deficient in such essential vitamins, and the increased parasitism of late winter and early spring may be a reflection of such dietary deficiencies. It may also be that certain of the helminth parasites present in large numbers in these deer had induced avitaminosis by interfering with normal assimilation. In this connection it may be significant that the two heaviest infestations were encountered on sickly captive young deer living under overcrowded conditions. Others of the same herd were healthy.

Helminth Parasites and Parasitic Diseases

Helminth parasites are almost universally present in deer and in the small concentrations normally encountered they probably have little or no effect upon the host. However, under certain conditions such parasites may increase to a point where they become a serious menace to the health of the host. At times they are apparently a contributory cause to, or the immediate agent responsible for, the death of deer.

There is convincing evidence that overcrowding, poor food conditions, and factors associated with juvenility and senility are among those predisposing deer to serious parasitism. There is also some suggestive evidence that complete absence of natural predators can foster an increase in the parasitism of deer.

Internal parasites of the digestive tract were recovered by screening the contents of the tract and supplementing this by opening and examining the tract for attached specimens of types such as *Trichuris*.

Numbers were ascertained by direct counting, which served satisfactorily with all species but *Capillaria*. This nematode became so entangled with the meshes of the screen that no reliable estimate of population could be made.

It was found virtually impossible, because of the time factor, to remove and count all individuals of lungworms from the bronchi and bronchioles of infected deer and with this parasite a less precise method of expressing the density of infestation was resorted to. In certain infestations of *Onchocerca* in which the worms were confined to the subcutaneous tissue, it was possible to estimate their numbers by direct count. However, if, as was often the case, the worms were lodged in the tendon sheaths and muscle fascia, this was not possible.

In certain cases thick blood smears were prepared and examined for filariae but this was not done for all specimens.

Oesophagostomum venulosum Rudolphi

The caecal worm is a widely distributed and abundant parasite of the coast deer throughout the parts of its range that have been investigated.

Van Roekel (24) found it abundant in California and it has been present in 25 of the 40-deer sample examined in this study in southwestern British Columbia, as well as in many other specimens from the study area. The small, rather thick worms are found most abundantly in the caecum but large numbers also occur in some cases in the upper colon and, occasionally, a lesser number in the lower ileum.

Heavy infestations seem to be concentrated in the winter and spring (see table) as such have been encountered in January, February, March, May, and June, while there have been no cases of heavy infestation among the summer and autumn deer examined. That this small number of cases may represent an actual condition is further supported by the findings of Swales (23) who shows a rising incidence in infestations of *O. columbianum* in sheep during the late winter and spring months.

No gross lesions resulting from the presence of this worm have been observed but it seems significant that while some diseased deer have light, or no infestations of this worm, all deer with heavy infestations have been in a seriously impoverished condition. Symptoms here attributed to oesophagostomiasis venulosum are those of general debility, pale mucous lining of the mouth, extreme emaciation, unkempt pelage, lassitude, and chronic diarrhoea accompanied by soiling of the buttocks, hocks, and tail (Fig. 1). In excess of 300 worms seems to constitute a serious infestation.

In one case of long-standing enteritis examined June 4, 1940, the deer was found on post-mortem examination to support a large population of *O. venulosum*. The tissues of this animal were anaemic, the liver about one-half normal size, hard, and dark, the veins of the intestine congested, and the mesenteric lymph nodes enlarged and dark red. Dietetic factors are thought to have been responsible for the anaemia and there is reason to believe that they may be frequently, if not universally, a predisposing influence in cases of oesophagostomiasis.

Another complicating factor in assessing the symptoms produced by *O. venulosum* is the presence of lungworm. Among the animals examined each deer with heavy *Oesophagostomum* infestation has had also at least a moderate lungworm infestation and every serious case of verminous pneumonia has been accompanied by a large population of *Oesophagostomum* in the caecum and large intestine. In the case just discussed, 30 lungworms were removed from the smaller bronchi and there were scattered collapsed areas in the dorsal lobes of both lungs. However there was no secondary infection discernible and no pneumonic changes visible. The total collapsed area was not more

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FIG. 1. *Adult female coast deer exhibiting extreme emaciation accompanying Oesophagostomum and Dictyocaulus infestation.* FIG. 2. *Dissection to show lung with pale area of normal tissue (x) and dark pneumonic area resulting from lungworm (Dictyocaulus viviparus) infestation.* FIG. 3. *Lung of coast deer containing two hydatid cysts (Echinococcus granulosus).* FIG. 4. *Multiple fibromata in female coast deer from Newcastle Island, B.C. (Photo by A. Peake.)* FIG. 5. *Multiple fibromata in male coast deer from Victoria, B.C.* FIG. 6. *Micromelic dwarf coast deer taken at Duncan, B.C., in 1931.*

PLATE I

than one-tenth of the lung and other cases suggest that such relatively mild lungworm infestations are not sufficient in themselves to produce the symptoms manifest by this deer.

Coming as it does during the period of severest environmental strain upon the deer as a result of cold weather, snow, and food deficiency, oesophagostomiasis is a serious contributory factor in the winter kill and at the same time, along with other debilitating diseases, probably renders the deer more vulnerable to predation.

Trichostrongylus sp.

A single specimen of a worm identified as of this genus by Dr. W. E. Swales was taken from the small intestine of a two-year-old male shot at Goldstream Lake. *Trichostrongylus* has not previously been reported from North American deer.

Ostertagia circumcincta (Stadelmann)

This worm, frequently a serious parasite of the abomasum of sheep, was of infrequent occurrence in Vancouver Island coast deer, even where these had contact with sheep. Two deer contained very small numbers (less than 12) of these worms in the abomasum and small intestine. Both were from the Goldstream area upon which there were no domestic sheep. One of two deer from Hardy Island contained three specimens.

Nematodirus filicollis (Rudolphi)

This parasite was encountered six times in the 40-deer sample examined. All occurrences were between Dec. 27 and May 21. Only one of the deer bore a heavy infestation. This, a sickly fawn in captivity on Salt Spring Island, was found to contain about 960 *Nematodirus* in the small intestine. Inasmuch as the same deer supported a very heavy louse population and a serious infestation of *Oesophagostomum*, it was difficult to say what part the *Nematodirus* played in inducing the impoverished condition.

Nematodirella longispiculata antilocaprae Dikmans

A wild fawn from Goldstream Lake, shot Dec. 27, and a captive fawn killed Jan. 25 provided the only occurrences of this parasite. Four hundred and fifty worms were present in the first, 175 in the second. In both deer *Nematodirus* was also present.

This is a blood sucking worm and when present in numbers it doubtless contributes to the general debility characteristic of heavy parasitism. At the same time its feeding punctures may provide harmful bacteria with means of access to the deeper tissues of the digestive tract.

The fawn with the heaviest infestation was in moderately good condition considering the season, and was larger than average. The other case, however, was on point of death from multiple parasitism that had followed upon improper weaning.

Dictyocaulus viviparus (Bloch)

Four species of lungworm are recorded from the Columbian black-tailed deer by Dikmans (4). These are *Dictyocaulus filaria*, *D. viviparus*, *Protostrongylus macrotis*, and *Elaphostrongylus odocoilei*. To date only the one species has been found in British Columbia but this is an abundant and serious parasite.

Thirty per cent of my 40-deer sample from the normal population on southern Vancouver Island bore more or less serious lungworm infestations, while many other infected deer were examined from Gambier, Bowen, and Hardy Islands as well as from Vancouver Island.

This parasite is one of the most important attacking the coast deer. From time to time it has caused serious losses, particularly to insular populations living in predator-free environments.

In the late winter and spring of 1928 an epidemic of verminous bronchopneumonia destroyed many deer on Bowen Island. Another outbreak removed a large part of the deer population of Gambier Island in the winter of 1942–43, while in 1941–42 almost the entire fawn crop on Bald Mountain game reserve succumbed to the attacks of this lungworm.

This worm was present in all seasons but deaths from its activities usually took place in the late winter and spring. Fatal cases were more frequent in deer less than one year old than in those of any other age group; though the parasite occurred in deer of all ages.

There was considerable variation in the symptoms visible upon post-mortem examination. Most frequently small areas on the free margins of the diaphragmatic lobes of the lungs were hard to the touch and pale in appearance. Such consolidation was sometimes accompanied by a number of greyish or yellowish cysts apparent on the lung surface. In other cases examined, a large part of the lung was hard and pale as a result of hypertrophy of the fibrous tissue in the walls of bronchi and bronchioles in response to the irritation produced by the worms. Occasionally the hard areas were inflamed and accompanied by local hepatization of the margins of one or both lungs. Adhesions occurred frequently.

The masses of worms occupied the lower trachea and bronchi in a catarrhal exudate of frothy mucous, often with traces of blood. Eggs and larvae were present in the respiratory tract.

The inflamed and weakened lung tissues apparently often suffer secondary bacterial infection that not infrequently culminates in either broncho- or lobar-pneumonia. In two cases of verminous pneumonia encountered on southern Vancouver Island the lungs bore numerous pus areas, greenish yellow in colour. Histological examination of the consolidated areas revealed an acute bronchopneumonia process. Numerous minute foci of fibrosis consisted of encysted lungworm larvae each surrounded by a dense fibrous capsule.

The frequent association of lungworm and *Oesophagostomum* infestations suggests that one of these worms may render the deer a more suitable host for the other.

A highly illustrative instance of the influence of predation upon diseased deer came to the author's attention at Brentwood, V.I., on Feb. 13, 1940. Here, after a short run of not more than one-third of a mile, a dog ran a yearling deer into the water. A swim of 150 yd. was all that intervened between the deer and the safety of the farther shore. There was no current and yet the deer swam feebly, grinding its teeth rhythmically and displaying obvious dyspnoea. It collapsed on the farther beach and made no attempt to resist capture. Rest and warmth failed to revive it and after two hours of panting, accompanied by grinding of the teeth, the deer died. Post-mortem examination revealed heavy lungworm infestation that had resulted in consolidation of about one-half of the lung tissue (Fig. 2). There were 250 *Oesophagostomum* in the large intestine.

On four other occasions during February the same thing happened at the same place. Three of the deer died, the fourth recovered in about eight hours and was released.

On Apr. 15, 1942, death of a yearling in Shawnigan Lake took place under identical circumstances.

It is obvious that the elimination of these heavily parasitized deer, daily distributing many hundreds of lungworm and other larvae over the range, was of considerable benefit to the game population. The occurrence provides a potent example of the role of cursorial predators in a population of coast deer.

Onchocerca cervipedis Wehr and Dikmans

The deer legworm is a rather common parasite of coast deer in southwestern British Columbia. In normal infestations the fine, thread-like worms often 8 in. or more in length are confined to the subcutaneous connective tissue and to the tendons of the shanks. Seldom do they extend above hock or knee and they are of more frequent occurrence on the hind than on the fore legs.

Fourteen deer of the 40 examined had this parasite. Two of these bore heavy populations and in these the worms were found in the intermuscular and subcutaneous connective tissue of the legs, sides, and even on the back, though they were progressively less abundant on the regions further removed from the lower legs. Each of these deer was estimated to support in excess of 200 worms.

On Gambier Island in 1927 there was a severe infestation of these worms in a large proportion of the deer; so much so that the worms were obvious to hunters and in consequence many deer were left in the woods after being shot.

Rush (19) records an ulceration of the shank in mule deer apparently resulting from the presence of this worm. The ulcer was found to contain numerous larvae. To date, no deleterious effects upon the host chargeable

to the presence of *Onchocerca* have been noted in British Columbia. There has never been even local inflammation in the region surrounding the parasite.

The larvae are discharged into the connective tissue and spaces adjoining the worm and are doubtless ingested by various biting flies and thus transported from host to host.

Setaria cervi (Rudolphi)

This filarial worm of the coelomic cavity is widely distributed throughout the range of the coast deer. It occurred in 21 of the animals examined in this study but usually only a small number of individuals was present in each host. The greatest number encountered was 55 in the coelomic cavity of a six-months-old fawn in captivity under overcrowded conditions.

The adult worms are to be found in the abdominal cavity, moving over the surface of the viscera and mesenteries. None was found anterior to the diaphragm. They appear to be harmless to the vertebrate host.

The larvae of this worm enter the blood stream where it was found from May through the summer but not in the winter months. Though the life history is imperfectly known, biting flies are the agents of transport from one vertebrate host to another and doubtless act as true intermediate hosts. A captive deer in Victoria, apparently exposed to the attacks of *Stomoxyx calcitrans*, the biting house fly, only, was found to have *Setaria* in the body cavity. Accordingly this fly is thought to be one intermediate host. However, *Stomoxyx* is not found among the wild deer away from civilization and there must be other suitable intermediate hosts among the horse flies, deer flies, black flies, and mosquitoes that are endemic to the area.

Elaeophora schneideri Wehr and Dikmans

An aged buck deer taken at Chemainus, V.I., on Mar. 19, 1940, provided the first specimens of this worm encountered. Unfortunately they were not discovered until after the deer had been decapitated during preparation of the skeleton. The worms recovered were all females and though their exact site was not determined there is little doubt that they were in the common carotid artery.

Living larvae were present in the oviducts of one of these worms and were doubtless present in the blood of this deer.

The only other record of this parasite in British Columbia was taken from a coast deer at Nanaimo, B.C. One worm, an immature female, was found coiled up between the peritoneum and the dorsal muscles of the abdominal cavity. There were no visible symptoms arising from the presence of this parasite.

Trichuris ovis (Abildgaard)

The whipworm of sheep occurs as a casual parasite of the coast deer on southern Vancouver Island. Single individuals were taken from the lower small intestine and caecum of four deer and five worms from a fifth. In the

latter, small haemorrhagic areas marked the site of attachment of the parasites to the mucosa of the caecum. The only other infected animal, a doe shot on Hardy Island on Apr. 3, 1943, contained 12 worms.

On the basis of present evidence it is doubtful whether this parasite ever becomes abundant enough to be of importance to coast deer living under natural conditions.

Capillaria sp.

This worm was taken from deer killed at Westholme, Duncan, and Goldstream on Vancouver Island. Five deer in all were found to have this minute worm, but on account of the inconspicuous nature of the parasite it is by no means certain that all cases of light infestation were recorded.

The maximum infestation was about 200 worms. All parasites were in the small intestine and no indication of injury to the host was encountered.

Fascioloides magna (Bassi)

This parasite has been reported from many parts of southwestern British Columbia but was rare in the area studied most intensively during the present investigation. Many hunters have reported shooting deer with 'swamp liver', the popular term for fascioloidiasis, in the vicinity of Courtenay, the Alberni valley, and from the Englishman's River valley.

One collection, made by A. Peake of Duncan, V.I., from a buck shot at Hilliers, V.I., consists of 23 flukes ranging in length from 30 to 40 mm. after preservation. The buck was fat and in good condition despite large-scale destruction of liver tissue.

The only infestation examined by the author consisted of a single encysted and disintegrating fluke taken from the liver of a three-year-old doe shot at Goldstream on Aug. 16, 1940. The liver had developed adhesions to the diaphragm.

Swales (22) found that deer constitute the normal host of *Fascioloides* and apparently suffer little inconvenience from small or moderate infestations. Heavy populations, however, constitute an important cause of losses to the coast deer in southern British Columbia. One such epidemic on Texada Island was recorded by Kermode (15).

This is another parasite that apparently renders the host vulnerable to the attacks of cursorial predators. In November, 1927, A. Peake was invited to accompany the game warden from Courtenay to examine the depredations of domestic dogs in the Kye Bay area. Nine recently dead deer were found along the beach. They had been run but not mauled by the dogs. Upon dissection it was discovered that each had died of haemorrhage into the body cavity, apparently from rupture of some part of the hepatic portal system. All the deer were heavily infected with liver fluke and there seemed little doubt that these parasites had been the cause of the venous rupture under heavy exertion.

Hadwen (9) records the sheep liver fluke, *Fasciola hepatica* L., from the black-tailed deer, *O.* [*h.*] *columbianus*, on the authority of F. Kermode. Inquiry of Mr. Kermode reveals that *F. hepatica* was merely a speculative identification of liver flukes in deer. In all probability the species was *F. magna*.

Moniezia benedeni (Moniez)

This was the only tapeworm found in the intestine of the coast deer on Vancouver Island. It was found in 10% of the deer examined but as there was seldom more than a single worm present in each host its effect was probably negligible.

Mature worms were taken in two six-months-old deer killed Dec. 9 and Jan. 25 and immature worms in an adult buck taken Oct. 31, 1939, and a yearling doe killed June 24. The heaviest infestation consisted of four worms in a five-months-old doe and five in an adult buck.

Each of two deer examined from a captive herd contained this parasite. These deer were confined in a small pasture and the presence of so small an infestation (one worm in each host) suggests either that this deer is not a highly favourable host or that some essential intermediate host was scarce.

Severe teniasis in sheep is known to cause weakness and digestive derangement that may end fatally but there is no indication of this worm becoming a serious pest of the coast deer.

Thysanosoma actinoides Diesing

This tapeworm has been recorded from three North American deer of the genus *Odocoileus* by Dikmans (4). Shaw and co-workers (20) found it in a deer from Douglas County, Ore., and Guberlet (in litt.) informs me that it is fairly numerous among coast deer on the Olympic Peninsula of Washington.

To date it has not been encountered on Vancouver Island and was taken but once on the mainland adjacent to Vancouver, B.C.

Cysticercus tenuicollis Rudolphi

In addition to the above two species of tapeworms for which the coast deer in British Columbia is the definitive host, this deer is intermediate host for three other species. *Cysticercus tenuicollis*, the asexual stage of *Taenia hydatigena*, a tapeworm of carnivores, is the most abundant of these.

It occurred in 33 of the 40-deer sample as well as in many other individuals. Frequently only one or two cysts would be present but larger infestations were not uncommon. Twenty-three was the largest number removed from a single host.

The fluid-filled cysts were usually attached to the greater omentum but were found also in a variety of other situations. One hundred and forty-five specimens were taken from the 40 deer examined and these were distributed as follows: greater omentum, 114; diaphragm, 9; lungs, 7; mesocolon, 6; liver, 4; pericardium, 2; peritoneum, 2; pleural peritoneum, 1.

It is quite usual to find from 2 or 3 to 15 or more small, more or less pedunculate cysts attached to the wall of the rumen. A number of these were examined microscopically and they appeared to be degenerate bladder worms. Occasionally these cysts were soft but more frequently the core was thoroughly calcified.

An attempt has been made to determine the definitive hosts of this tapeworm on southern Vancouver Island. In the course of this investigation, the writer examined seven feral house cats, five dogs, one timber wolf, four mountain lions, two raccoons, four bears, two bald eagles, four ravens, two turkey vultures, and one red-tailed hawk, all captured at or in the vicinity of deer offal. For the most part these examinations were negative in so far as *T. hydatigena* was concerned. However, it was present in three mountain lions, two dogs, and the timber wolf. The two last are well known as hosts of the parasite but it has not hitherto been reported from the mountain lion.

Mountain lions are scarce in the area from which the deer for this study were obtained. Too scarce, in fact, to have been responsible for the observed incidence of *C. tenuicollis*. Furthermore, the parasite is abundant on Salt Spring Island upon which there are neither bears, mountain lions, nor wolves. At the present stage of the investigation then it seems probable that dogs are the usual definitive host transmitting this parasite to the deer.

On Pitt Island the one deer examined supported no parasites other than a single cysticercus of this tapeworm. Here wolves are abundant and as no other mammalian predators are present, they are almost certainly the definitive host.

Light infestations with these cysticerci seem to do little damage to the host but exceptionally heavy infestations can cause death. An instance of this is recorded for *O. h. hemionus* by Gregson (8). In the case reported upon the deer was confined in a pen to which dogs had access. Its lungs, liver, and omentum were obscured by the hundreds of cysticerci present on them.

Cysticercus ovis Cobbold

This bladder worm was encountered once only. On Nov. 18, 1943, a sample consisting of 196 gm. of flesh from the haunch of a deer taken at Menzies Bay, V.I., was received. Embedded in the muscle tissue were 10 cysts of *C. ovis*. The muscle tissue of both hind legs was reported to be parasitized to approximately the same degree.

Echinococcus granulosus (Batsch)

The single instance of this parasite in the coast deer in British Columbia occurred at Crofton, V.I. A two-year-old buck in good condition taken there Oct. 8, 1939, bore a large and a small cyst of this worm in its left lung (Fig. 3). In this region the deer were grazing over the same ground as domestic sheep.

Discussion of Parasitism

During the present study 25 species of arthropod and helminth parasites have been recorded from the coast deer in southwestern British Columbia. Twenty-one of these occurred in a random sample of 40 wild deer from southern Vancouver Island. The most widespread parasite was *Lipoptena depressa*, present on 95% of the deer examined (see Table II), but this is closely followed in incidence by the bladderworm, *Cysticercus tenuicollis*, 83%, and the biting louse, *Tricholipeurus virginianus*, and *T. parallelus*, 73%.

TABLE II

INCIDENCE OF INFESTATION WITH 21 SPECIES OF PARASITES IN A RANDOM SAMPLE OF 40 COAST DEER FROM VANCOUVER ISLAND

Species	Organ	Number of possible occurrences	Times occurred	Deer infected, %
Ixodes californicus	Skin	18	6	33
Dermacentor albipictus	Skin	24	11	46
Cephenemyia jellisoni	Nose and pharynx	40	12	30
Lipoptena depressa	Skin	40	38	95
Tricholipeurus sp.	Skin	40	29	73
Cervophthirius ferrisi	Skin	40	2	5
Fascioloides magna	Liver	40	1	3
Cysticercus tenuicollis	Mesenteries and liver	40	33	83
Echinococcus granulosus	Lungs	40	1	3
Moniezia benedeni	Small intestine	40	4	10
Oesophagostomum venulosum	Caecum and colon	40	25	63
Trichostrongylus sp.	Small intestine	40	1	3
Ostertagia circumcincta	Small intestine	40	2	5
Nematodirus filicollis	Small intestine	40	6	15
Nematodirella longispiculata	Small intestine	40	1	3
Dictyocaulus viviparus	Lungs	40	12	30
Onchocerca cervipedis	Legs	40	14	35
Setaria cervi	Coelom	40	21	53
Elaeophora schneideri	Blood vessels	40	2	5
Trichuris ovis	Small intestine and caecum	40	5	13
Capillaria sp.	Small intestine	40	5	13

So far as is now known only five of these parasites induce recognizable disease in the host. Experimental proof is lacking for even these, but by inference from field evidence, *Cephenemyia jellisoni*, *Oesophagostomum venulosum*, *Dictyocaulus viviparus*, *Fascioloides magna*, and *Nematodirus filicollis* are apparently often responsible for serious parasitic disease not infrequently fatal.

Multiple parasitism is the rule in the coast deer in southern British Columbia. Of 45 deer examined in their entirety, all bore more than a single species of parasite. The mean was six species and 11 was the greatest number of species taken from a single deer. Fig. 7 gives the distribution of numbers of parasite species in graphic form.

Olsen and Fenstermacher (18) working with the white-tailed deer in Minnesota found that those of yearling age or less were almost devoid of helminth

parasites, but were host to relatively large populations of ectoparasites. On Table III, the occurrence of each of 21 species of parasites recovered from coast deer on southern Vancouver Island is examined in relation to the age group of the host. It will be noted that in this deer the young

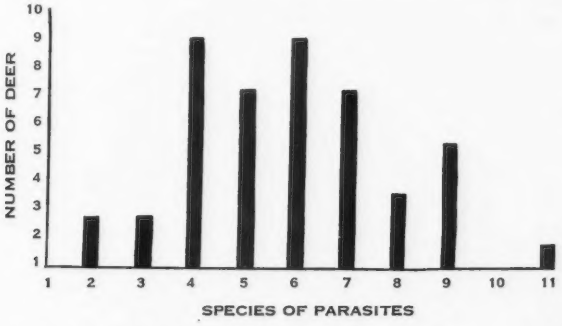

FIG. 7. *Graph showing numerical distribution of species of parasites in 45 deer.*

TABLE III

AGE DISTRIBUTION OF PARASITE INFESTATIONS AMONG 44 COAST DEER FROM SOUTHERN VANCOUVER ISLAND, B.C.

	12 deer under one year old		32 adult deer	
Ixodes californicus	1	10%	5	16%
Dermacentor albipictus	1	10%	10	31%
Cephenemyia jellisoni	6	50%	10	31%
Lipoptena depressa	9	70%	29	91%
Tricholipeurus sp.	7	60%	24	75%
Cervophthirius ferrisi	1	10%	1	3%
Fascioloides magna	—	—	1	3%
Cysticercus tenuicollis	9	70%	28	87%
Echinococcus granulosus	—	—	1	3%
Moniezia benedeni	1	10%	4	13%
Oesophagostomum venulosum	7	60%	21	66%
Trichostrongylus sp.	—	—	1	3%
Ostertagia circumcincta	1	10%	1	3%
Nematodirus filicollis	5	40%	2	6%
Nematodirella longispiculata	2	20%	—	—
Dictyocaulus viviparus	6	50%	9	28%
Onchocerca cervipedis	—	—	14	44%
Setaria cervi	9	70%	16	50%
Elaeophora schneideri	—	—	2	6%
Trichuris ovis	1	10%	4	13%
Capillaria sp.	1	10%	4	13%

are, in general, almost as frequently parasitized by helminths as are the adults, although they have yielded only 16 species of parasites as opposed to 21 in the mature animals. There are, however, certain differences in incidence that appear significant even on the basis of the small number of individuals examined. The much higher incidence of *Cephenemyia* in the young than in

adult deer may reflect the inexperience of the young in preventing the adult fly from larvipositing. The mature deer by constant movement, or by sheltering the nostrils against the ground and behind the forefoot, or by bedding in the deep, cool recesses of swamps, do much to avoid the attacks of this fly. Except for the choice of bedding sites the fawns have not been seen to fight the fly as consistently as the adult deer.

The more frequent occurrence in young deer of lungworm (*Dictyocaulus*), 50% as against 28%, *Nematodirus*, 40% as against 6%, and *Setaria*, 70% as against 20%, probably is a direct result of a greater susceptibility in deer less than one year old.

Onchocerca is notable as abundant in adult deer but not as yet taken from the yearlings.

Quite apart from the observable symptoms of disease produced by certain parasite infestations, it has been shown by Keys (16) that even apparently minor parasitism can significantly reduce the viability of a host confronted with adverse circumstances. It is well known also to stockmen that weight increment in parasite-free sheep is significantly greater than in sheep supporting even moderate populations of helminths.

It is probably justifiable then to assume that the presence of widespread multiple parasitism in the Vancouver Island deer population renders the parasitized individuals more vulnerable to adverse circumstances. The most frequently encountered of these adverse circumstances are winter climatic and food conditions and natural predation. There has not been opportunity during this study to examine carcasses of many winter-killed animals to determine the degree and nature of their parasite infestations in comparison with the sample taken from the normal population. Apparently this has yet to be done in any part of North America.

Evidence so far available suggests that the cursorial predators, such as the *Canidae*, that catch their prey by running it down, selectively remove heavily parasitized individuals. Of 10 deer dead as a result of pursuit by dogs, nine were heavily parasitized as against one that was virtually parasite free. There was no opportunity of inquiring into the position of stealth-predators such as mountain lion in this respect.

Diseases, Injuries, and Anomalies

During the course of the study of parasitic diseases of the coast deer several non-parasitic diseases, injuries, and other anomalies have come to the writer's attention. Except for certain dental conditions, dealt with in a later section, and one instance of arthritis, none of the departures from the normal described here occurred in the random sample from Vancouver Island. Most of the cases were sent to me by game wardens or hunters and thus were selected from among several thousand normal deer. Even collectively, the conditions described in this section have occurred so infrequently in southern British Columbia that they can have little or no effect upon the deer population.

It is possibly significant to note, however, that four apparently congenital defects of the limbs have arisen in the Vancouver Island population while no similar conditions have as yet been reported from the much larger deer population on the mainland coast.

Later in this paper it will be shown that the Vancouver Island deer have also a higher incidence of tooth anomaly than has been found in any mainland area.

Insular isolation of deer is known to result in reduced body size, certain changes in cranial form, and an increased tendency toward albinism. The conditions described in the present paper may be additional reflections of the same influence.

Neoplasia

Neoplasms were not encountered in the random sample of 40 deer given necropsy and parasite examination. They were recovered, however, from nine other deer during the course of this study. Three of these bore papillomata, four multiple fibromata, while two were not examined histologically.

Papilloma

A two-year-old buck shot at Malahat Station, Vancouver Island, B.C., in November, 1936, bore a number of papillomata on the skin surrounding the right eye. The largest tumour measured 15 mm. in diameter.

Four other instances of epithelioma of an apparent papillary nature came to my attention. Two of these were examined histologically.

Fibroma

Five deer with multiple fibromatosis have come to my attention between 1936 and 1941. A two-year-old buck from Happy Valley, a yearling buck from Prospect Lake, a yearling buck from near Mount Finlayson (all localities adjacent to Victoria, B.C.) a two-year-old buck from near Cobble Hill, and an adult doe from the Nanaimo district all bore large numbers of tumours (Fig. 4).

The yearling buck from Mount Finlayson was typical of deer bearing multiple fibromata. In this animal the largest tumours, many of them from 2 to 4 cm. in diameter, were situated on the head, neck, and shoulders (Fig. 5). Some of these large tumours were pedunculate, others were sessile, several of them were suppurating. Large tumours surrounded the eyes, where they obstructed vision, others around the antler bases almost obscured the small spike antlers. The surface of the body was studded with tumours that became smaller posteriorly on the body and distally on the limbs.

Laminitis

The overgrowth of one or more hoofs of otherwise apparently normal wild deer was found twice. A buck shot at Sooke, V.I., in 1936 had all four hooves overgrown and recurving at the tips. Another adult buck shot at Sooke on Dec. 5, 1932, had only the left hind foot distorted in this way.

Peritonitis

The three cases of peritonitis examined were the result of gunshot wounds in the abdomen. In one, a .22 bullet had passed through the posterior part of the abdominal cavity piercing the caecum and colon and allowing their contents to escape into the coelom. The other two, a buck and a doe, had shotgun wounds in the abdomen.

Arthritis

The most outstanding case of arthritis examined was that of an aged buck that died naturally as a result of cervical dislocation. There was a large dentoalveolar abscess in the left mandible.

This deer shows pronounced chronic arthritis of the distal limb joints accompanied by some grooving of certain joints, extensive periarticular hyperostosis and some rarefaction of the bodies of certain long bones.

The vertebral column is not affected, nor are the ribs except for the first on both sides. The articular surface of the tuberculum of both these ribs shows some porosity and the distal extremity of the left one is slightly hypertrophied on its internal face. The posterior end of the penultimate sternabra is somewhat enlarged.

As was found to be the case in the arthritic artiodactyls examined by Fox (6), the posterior limbs of this specimen exhibit more pronounced lesions than do the anterior.

The left hind limb is apparently normal, as are the hip and shoulder joints and the right elbow joint. All others are more or less deformed.

In the right fore limb there is no apparent damage to the actual articular faces, but there is slight hyperostosis of the anterolateral face of the radius at its distal end. Similarly there is some hyperostotic deformity of the medial (to the animal) face of the scaphoid, the anterior face of the lunatum, the anteroexternal face of the triquetrum and the hamatum, the articular end of the pisiform, and the anterior face of the canon at its proximal end. There is slight swelling and porosity of the proximal ends of the first phalanges and some osseous overgrowth of the periarticular area of the terminal phalanges of digits 3 and 4.

Besides some hypertrophy of the epiphyseal region at the distal end of the left humerus this bone bears a small eroded lesion on the articular surface of the lateral condyle that suggests ulceration. The proximal end of the left radius bears a bony ridge along the anterior epiphyseal margin. A similar

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FIG. 8. *Sternum of fawn born with three legs.* FIG. 9. *Ventral aspect of sacrum of fawn born without a left hind leg. Note incomplete fusion of arcualia and anomalous form of the vertebrae.* FIG. 10. *Normal (right) and deformed (left) calcaneus and astragalus of male deer B.C.M.Z. No. 469 with arthritis. Note deformity of calcaneus and grooving of proximal articular surface of astragalus.* FIG. 11. *Atlas, with part of axis in position, of B.C.P.M. No. 4589. Note hyperostosis opposite tip of spine of axis.* FIG. 12. *Distal end of left tibia of B.C.M.Z. No. 469 with hyperostosis accompanying arthritis.* FIG. 13. *Posterior view of atlas of No. 4589 showing displacement of odontoid notch.*

PLATE II

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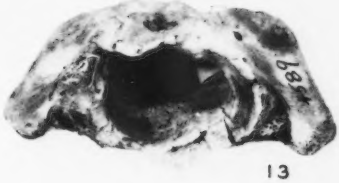

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ridge surrounds the articular surface of the semilunar notch in the ulna while there is marked porosity in the olecranon immediately behind the notch.

In addition to the deforming periarticular hypertrophy surrounding the distal end of the radius, there is extensive destruction of the articular surfaces, particularly of the radiolunar and radiotriquetral articulations. The latter shows erosion and scoring.

In the left radiocarpal joint there is luxation, erosion, scoring, and deformity of articular surfaces and marked hypertrophy particularly of the scaphoid. The proximal end of the canon exhibits epiphyseal hyperostosis and the rarefaction of its proximal external surface gives evidence of inflammatory processes. The digital elements are but slightly or not at all distorted.

Except for some epiphyseal hypertrophy at the knee and in the tarsals, the right hind limb is normal.

The heel joint of the left hind limb is deformed almost beyond recognition (Figs. 10 and 12). Pronounced luxation is evident and is accompanied by destruction and grooving of the proximal articular surface of the astragalus, calcaneus, and third cuneiform and false ankylosis between the latter and the naviculocuboid.

The only other case of arthritis encountered involved the atlas and axis of an adult doe, B.C.P.M. No. 4589, shot for parasite examination, on southern Vancouver Island. In this deer there is subluxation of the atlas to the right. This subluxation apparently arose during the early formative period of the bones involved for it accompanied pronounced distortion of the axis. The left anterior articular facet is extended to the right of the mid-ventral line and the right one correspondingly reduced. There is a deep odontoid notch on the left posterior articular surface of the atlas. Hyperostosis has taken place on the dorsal arch of the atlas and the anterior tip of the spine of the axis. The odontoid and bases of the transverse processes of the atlas posteriorly are porous (Figs. 11 and 13).

No other lesions were observed in the skeleton of this animal but the posterior half of the axis and cervicals 3 and 4 were destroyed at time of death and may or may not have been somewhat deformed.

It is of interest that these are the first two reported cases of arthritis in *Odocoileus* living under wild conditions.

Fractures

Fractures are probably among the more frequently suffered injuries. Many are the result of bullet wounds received during the hunting season. However broken bones frequently arise as a result of mishap during the normal activities of the animal.

In the author's collection are a fractured femur from a buck (*O. hemionus*) shot near Vernon, B.C., in 1931 (Fig. 16), and a metatarsal (canon) from Sooke Lake, V.I., B.C., taken from a buck shot by E. Peden of Victoria. Both these apparently resulted from bullet wounds. In the first, misalign-

ment followed by healing had foreshortened the femur to a degree that the leg was no longer useful. In the latter case a simple fracture without displacement had resulted in a perfect union with moderate callus formation. The injured limb was slightly deformed as a result of an anterior bending of the limb distal to the fracture. Fragments of the bullet are embedded in the bone.

Two other fractures do not appear to have been caused by bullet wounds. An aged buck shot at Chemainus, V.I., B.C., Mar. 19, 1940, was found to have a healed fracture of the seventh and fifth costal cartilages. These had been calcified at the time of injury and the broken ends had become united in an overlapping position.

A yearling buck found recently dead at Goldstream Lake on Dec. 19, 1939, had a comminuted compound fracture of the left tibia 5 cm. distal to the knee. The pointed extremity of a dead bone fragment projected from the wound with its internal end loosely held in the callus (Fig. 15). Despite much new bone formation the fractured bone had not united. The deer had succumbed to the debilitating effects of the injury and was in an extremely emaciated condition. Its antlers had been shed almost a month ahead of schedule.

An adult doe belonging to a semi-tame but unconfined herd at Cowichan Lake suffered a double fracture of the distal end of the left fore canon bone in mid-July 1941, about two weeks after the birth of her twin fawns. According to Mr. Buchanan Simpson, owner of the property favoured by these deer, the injured leg became greatly swollen for a period of two or three weeks, after which the swelling subsided and healing took place. By November the deer was using the limb again.

As a result of her injury the doe was unable to nurse her fawns satisfactorily. Premature weaning so stunted and weakened the young animals that they died at the onset of cold weather.

Blindness

Occasional instances of blindness following upon ulcerative keratitis and pink eye have been reported from California but no such cases have come to the writer's attention.

In July, 1936 a young fawn brought to the Saanich game farm near Victoria, B.C., was evidently almost completely, if not completely, blind. It did not react to normal visual stimuli and was unable to avoid objects in the environment. There were no obvious lesions of the cornea, but the specimen was not made available for study of the eyes and their innervation in more detail.

Careful tending enabled this fawn, a female, to reach the age of 18 months when she was killed by another doe. Deer have been noted to be vicious toward any incapacitated members of their species and this instance serves to emphasize the fate of individuals unable to avoid the attacks of others.

FIG. 14. *Normal and abnormal hind feet of deer with unilateral hemimelus. Duncan, B.C.* FIG. 15. *Comminuted compound fracture of the tibia. Goldstream Lake, B.C., Dec. 19, 1939.* FIG. 16. *Healed fracture of the femur from dorsal aspect. Vernon, B.C., 1931.* FIG. 17. *Male B.C.P.M. No. 4719 with anomalous* PM^3.

PLATE III

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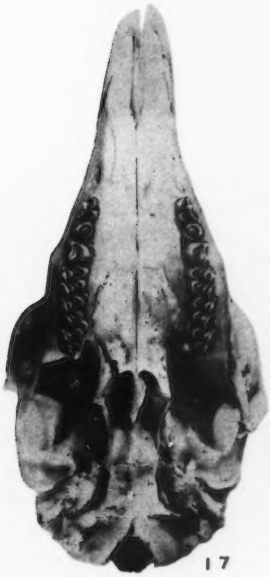

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Hemimelus

An instance of unilateral malformation of the hind leg apparently classifiable as hemimelus occurred in an adult buck shot near Duncan, V.I., B.C., on Sept. 4, 1941. In this animal the right hind leg was normal as far down as the proximal end of the canon but progressively foreshortened distal to that point. Upon gross examination it was apparent that the anomaly had operated primarily upon the skeleton and to a much smaller degree upon the skin. The skin appeared bunched onto the limb at its distal end, with the result that it was somewhat thicker there, the hair was more erect as if crowded together, and in furtherance of this effect the metatarsal gland, though of identical length on both hind limbs, was in a curved position on the anomalous one thus shortening its dorsoventral dimension. The two external digits were almost normal in development but the two median ones were missing, the leg ending in a stump covered with blackish, hairless, slightly cornified skin.

The canon is much foreshortened and somewhat hypertrophic distally, the body of the bone is only partially ankylosed with the two trochlear elements, which, on their ventral surfaces, show sufficient of their normal form to render the distorted rudiments identifiable. The trochlear elements are themselves co-ossified and are also ankylosed with the rudiments of the proximal phalanges of digits 3 and 4. The two pairs of proximal sesamoids are only slightly distorted as also are the phalanges of the external digits (Fig. 14).

The deer had apparently suffered little inconvenience as a result of the foreshortened limb and was in good health. Such a condition would render the possessor highly vulnerable to predator attack in a normal environment. This deer, however, was living in an almost predatorless area. Inasmuch as most limb anomalies of this type are known to be strongly inheritable, rapid predator elimination of such individuals can be considered beneficial to the race.

Amelus

In June, 1942, loggers at Cowichan Lake, V.I., found a three-legged fawn. It was only a few days old but apparently in good health. After three weeks of captivity it weakened and died. Myiasis of the rectum was a contributory cause of death.

The left hind leg had not developed and the skin covering the region where the leg should have been was black and hairless. The rectum protruded on the legless side. Examination of the skeleton revealed that the left innominate and all leg elements were absent and that there were structural defects of the left transverse processes of the sacral vertebrae and a sigmoid distortion of the sternum (Figs. 8 and 9).

Micromelic Dwarfism

Two dwarf deer have been captured alive on Vancouver Island during the last 15 years, one at Duncan and one at Nanaimo. Unfortunately both were killed and the carcasses destroyed without dissection. Both were does

and of approximately normal body size but with extremely short legs. The latter feature rendered them so ineffective in the bush that they were easily run down and caught by hand. It will be noted from Fig. 6, which depicts a doe taken at Duncan in 1931, that the foreshortening of the legs has followed the same pattern already described for the case of hemimelus from the same area. That is, the legs depart from the normal in progressively greater degree in a distal direction with the hoofs of the main digits virtually absent.

Variations and Diseases of the Teeth and Jaws

Variations in numbers of teeth in the genus *Odocoileus* are rare. In *hemionus* one instance of a supernumerary incisiform tooth has been seen. Specimen No. 4958 in the Museum of Vertebrate Zoology, Berkeley, Calif. has nine teeth in the lower incisiform row instead of the normal eight. M.V.Z.* specimen No. 59936 has a partially erupted supernumerary cusp between the roots of the second lower molars in each mandible (Fig. 24).

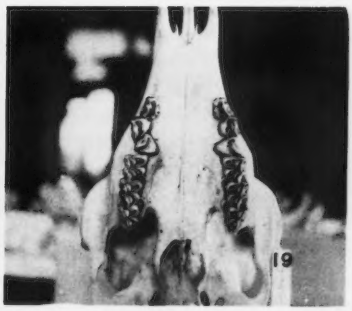
The only other variation in number of teeth encountered is the occasional presence of upper canines. This condition has been recorded by Nordquist (17) as occurring in two mule deer (*O. h. hemionus*) in California. There can be little doubt that this condition is an atavism occurring as an infrequent genetic variation or combination in the normal population. The above author found the two instances recorded in an examination of approximately 4000 deer, an incidence of 0.05%.

Radical departures from the normal as regards form of the tooth are also infrequent, and only one instance has been seen in about 400 specimens. An adult male coast deer taken near Duncan, V.I., B.C., in 1940 has PM^3 on both maxillae departing widely from the usual pattern (Fig. 17). In these teeth the cross section is almost circular, rather than bluntly triangular, and instead of there being an internal crescent and external crest in contact, but not united, posteriorly in the unworn tooth, the enamel is continuous around the crown of the tooth and in the centre of the circle so formed is a circular column. The identical structure of these two teeth leaves little doubt that this variant has a genetic background.

While variations in number of teeth are rare, variations in position are comparatively frequent. The teeth most often involved are the third and fourth upper permanent premolars. As yet I have seen no position anomalies in the deciduous dentition.

* M.V.Z. *refers to the Museum of Vertebrate Zoology, Berkeley, Calif.*
B.C.P.M. *refers to the British Columbia Provincial Museum, Victoria, B.C.*
B.C.M.Z. *refers to the Museum of Zoology, Dept. of Zoology, University of British Columbia, Vancouver, B.C.*

FIG. 18. *Deer with faulty attrition and protusion of unworn teeth, the result of loss of opposing teeth. Nanaimo, B.C., 1939.* FIG. 19. *Rotation of the upper premolars in B.C.P.M. No. 4618.* FIG. 20. *Paradontal disease in female, B.C.P.M. No. 4559.* FIG. 21. *Dental caries in B.C.M.Z. No. 190.* FIG. 22. *Alveolar abscess following attrition in senile male B.C.P.M. No. 4664.* FIG. 23. *Ulcerated mandible in B.C.M.Z. No. 469. This deer had an advanced arthritic condition.*



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The position variant encountered most frequently is a rotation of the fourth upper premolar (Fig. 19). The rotation can take place in either direction but is most commonly internal (i.e. with the anteroexternal corner rotated inwardly). In this deer the anteroposterior diameter of the premolars is often the shortest of all possible diameters and as this is normally directed nearly parallel with the anteroposterior plane of the maxilla, rotation of the tooth frequently does not relieve an overcrowding. In certain instances, as in the right maxillary tooth row of B.C.P.M. No. 4618, rotation probably resulted from overcrowding and is associated with an internal displacement of PM^4 and slight external displacement and rotation of PM^3. In B.C.M.Z. No. 151, however, rotation of PM^4 on both maxillae so that the longest diameter (externolingual) is directed anteroposteriorly, has apparently been the cause of, rather than the result of, the overcrowding and has occasioned internal displacement of PM^3. PM^4 in B.C.P.M. No. 4618 shows internal displacement without rotation, a condition that may have been induced by the persistence, at the external posterior corner, of one fang of the deciduous PM^4.

Further instances of rotation of upper $PM^{3 \text{ and } 4}$ are as follows:

B.C.P.M. No. 4560—two-year-old ♂ from Crofton, V.I., B.C., has PM^3 rotated inwards about 90°.

No. 4665—two-year-old ♂, Goldstream, V.I., 30° rotation of both PM^3's.

I.McT.C. No. 427—four(+)-year-old ♂, Alberni, V.I., right $PM^{3 \text{ and } 4}$ and left PM^3 rotated inwards 45°.

No. 391—four(+)-year-old ♂, Comox, V.I., right PM^3 and PM^4 rotated inwards 45° and 30° respectively. This specimen also has PM_4 displaced toward the lingual side of the mandible. This is the only malplacement of a member of the lower molar row encountered.

The above six specimens with malplacement of one or more teeth were encountered in a group of 38 deer taken at random on southern Vancouver Island. This group does not include any that were brought to me because the teeth were noticed to be misplaced. If this small sample is representative of the island population, the deer on southern Vancouver Island have a higher incidence (16%) of tooth anomalies than any other population so far studied.

In a group of 91 adult deer from the mainland, three from British Columbia, one from the Olympic peninsula, Washington, and 87 from California, in the Museum of Vertebrate Zoology, Berkeley, Calif., there are only two with position anomalies of the teeth. A male, No. 23703, from Laytonville, Mendocino County, Calif., has PM^4 rotated on both maxillae. In ♀ No. 90337 from Alamo, Contra Costa County, Calif., left PM^2 is rotated 90°.

Persistence of the roots of deciduous premolars is not unusual. The posteroexternal fang of deciduous PM^4 is present in B.C.P.M. No. 4618 in the left maxilla accompanied by internal displacement of its permanent successor.

The same fragment is present in I.McT.C. No. 391 on the right side accompanied by internal rotation of the permanent PM^4. It is similarly present in both maxillae of the B.C.P.M. No. 4559 where very slight rotation of PM^4 on both sides is present. In this deer the posterointernal fangs have also persisted.

In the first two cases the presence of this persistent root might be considered to have resulted in the displacement of the permanent member, or the persistence might just as properly be attributed to the malplacement of the developing permanent tooth on the ground that the deciduous roots may not be absorbed in absence of pressure on the part of the developing successor. The small amount of rotation in the third instance in spite of the presence of a large vestige of the deciduous tooth suggests that the presence of such vestiges does not necessarily occasion misplacement of the permanent member.

Irregular Attrition

This type of tooth malformation may arise from several different causes. Broken teeth or sloughed teeth cause cessation of normal attrition of their partners on the opposing row. Under such circumstances the absence of wear soon results in this unopposed tooth exhibiting greater crown height than its neighbours. Such has been the case in B.C.M.Z. No. 469 already referred to. Here PM^4 and M^1 project below the general crown line as a result of loss from disease of M_1 on the same side, but as the injury was apparently suffered late in life the abnormal projection of the opposing members is slight. In this same deer, however, the bite was not perfectly aligned and in consequence M^3 on the right side has the posterior cusp and crescent unworn and projecting well below the normal crown line.

In a deer shot near Nanaimo in 1939 and examined in February, 1940, an injury early in the life of the animal had removed PM_4 and the anterior half of M_1. In this specimen not only have the opposing teeth remained unabraded but they have come to project further than normal from the alveolus (Fig. 18).

Broken teeth are infrequently encountered. In 106 California-taken deer of this race, just five instances have been noted. In one of these, a comparatively young deer, No. 54993, the entire lingual surface of M_2 has been broken away, the fracture extending to below the gum line. There is no indication of death of the tooth or infection of the alveolus, but inasmuch as the pulp cavity is exposed, infection must soon have occurred.

Diseases of the Teeth

I have encountered no *hypoplasia*, as defined by Colyer (2), in wild deer. Dentoalveolar abscesses are, however, not uncommon. One such instance is represented by an old adult male skeleton B.C.M.Z. No. 469 (Fig. 23). This deer died as the result of a dislocation of the cervical vertebrae apparently occasioned by a fall. Advanced arthritis of the lower limbs undoubtedly led to its fatal accident.

The left ramus of the mandible of this animal bore a deep-seated abscess that had invaded the body of the mandible, the pus eventually finding an exit low down on the external and internal surfaces. There is considerable swelling adjacent to the abscess. Ventrally this shows evidence of rarefying osteitis, whereas nearer the alveolar border the swelling is solid and is probably the result of a sclerosing osteitis. The appearance of the remaining fragments of M_1 suggest that fracture of this tooth may have opened the way to the infection. Necrotic changes are visible in the alveolus and anterior root of M_2. It is possible that the abscessed condition of the mandible was intimately associated with the arthritis deformans of the lower limbs and that the organisms responsible for the arthritis had gained access to the blood stream by way of the ulcerated alveolus.

B.C.P.M. No. 4664, a senile ♂ taken at Chemainus, V.I., B.C., has many of the teeth worn down to the gum line, M^1 on both sides was represented by the four disconnected roots, loosely held in position by the mucoperiosteum and underlying connective tissue (Fig. 22). There has been marked absorption of the roots of all teeth. An alveolar abscess involves the mandible in the vicinity of PM_4. The mandible here is swollen and the alveolar margins porous. The interalveolar septum has been destroyed between PM_4 and M_1.

Displacement of PM_4 in I. McT.C. No. 391, an adult ♂ from Comox, is associated with an abscess involving the alveolus of this tooth and adjacent PM_3 (Fig. 29). There has been considerable necrosis of the peridental tissue, and swelling of the mandible, accompanied on the external surface by porosity and on the lingual surface by sclerosis.

In a group of 106 specimens of adult *O. h. columbianus* from various parts of California, in the Museum of Vertebrate Zoology and California Academy of Sciences, six show dentoalveolar abscesses.

Male No. 54986, Van Duzen, Humboldt County, Calif., has abscesses involving the alveolus of M_1 and M_2 on each mandible accompanied by destruction of adjacent parts of these teeth and inflammatory changes in the circumscribing bone of the mandibles.

Male No. 65247, Stonyford, Glenn County, Calif., shows extensive destruction of the alveolus of the right upper second molar, exposing the external roots (Figs. 27 and 28). The alveoli of lower molars 1, 2, and 3 on both mandibles have been destroyed, the teeth are dark coloured and dead, several of them resting loosely in position. The abscesses have established exit holes on the lingual surface of the mandible. This is not an old deer, the teeth are not abraded, and there is no indication of the site of primary infection.

Male No. 65243, Yolla Bolly, Tehama County, Calif. Destruction of the alveoli of right PM_4 and M_1 together with the anterior segment of the latter and the posterior part of the former teeth.

Male No. 59936, Chico, Butte County, Calif., has a large abscess involving the external side of the alveolus of right M_3. The inflammatory area extends anteriorly along the border of the alveolar edge as far as PM_3.

Male No. 90596, Skunk Creek, Santa Clara County, Calif., is an old animal and the extensive abscess in the right mandible apparently began at M_1 as a result of mechanical injury to the gum, possibly associated with fracture of this tooth (Fig. 26). The same process in an earlier stage is evident in the left mandible. In the same specimen, left $M^{1 \text{ and } 2}$ also have dentoalveolar abscesses.

Examination of these dentoalveolar abscesses, eight in 156 deer, reveals that the mandibular tooth row is many times more vulnerable to infections of this nature than is the maxillary tooth row. Of the 13 tooth rows bearing abscesses, two were maxillary, 11 mandibular. Furthermore, in six out of the 13 tooth rows, the primary site of infection lay in the alveolus of M_1, in two it was between M_1 and PM_4, in one at PM_4, in one at M_3, in one at M^2, in one between M^1 and M^2, and in one was undeterminable. The first molars are, in the adult deer, the oldest teeth in the mouth, they are consequently the first to reach the end of their functional life and to thus expose the jaw to infection. Furthermore, the ventral contour of the maxillary tooth row varies from a gentle arc to a flat V with the apex at M^1. In the latter case the abrasion of M_1 is accelerated. It has been observed that deer with dentoalveolar abscesses in the region of M_1–PM_4 almost invariably present the angular outline of the upper tooth row. The indications are that abrasion of M_1 is the most important single factor leading to the formation of abscesses in the mandible and that old age, together with conformation of the maxillary tooth row, are responsible for the localization of the danger point in M_1.

I have found no dentoalveolar abscesses in immature or young deer.

In the one case obtained while culture of the infective organisms was still possible, *Actinomyces israeli* was isolated as the pathogen.

Caries

In an adult male, *O. h. hemionus*, from Telkwa, B.C., is the only case of caries I have encountered in approximately 750 wild-taken skulls (Fig. 21). In this specimen, B.C.M.Z. No. 190, the enamel of the posterior crest and anterior crescent of M_1 on the left side has been fractured and doubtless this accident resulted in the carious condition. The enamel lining the anterior lake has been partly destroyed as has that on the approximal surfaces in general, the enamel remaining is stained a dark brown, is rugose, and somewhat decalcified. There is indication of an inflammatory condition with some redeposition of bony material along the gum line on the lingual surface of the tooth. The inflammation has been operative also on the adjacent margin of the alveolus.

FIG. 24. *M.V.Z. No. 59936 with supernumerary cusp between roots of* M_2. FIG. 25. *M.V.Z. No. 54993 with fracture of the lingual surface of* M_2. FIG. 26. *M.V.Z. No. 90596 with abscess of mandible originating in alveolus of* M_1. FIG. 27. *M.V.Z. No. 65247 showing extensive alveolar destruction in molar rows.* FIG. 28. *M.V.Z. No. 65247 with alveolar abscess of* M^2. FIG. 29. *I.McT.C. No. 391, displacement of* PM_4 *with abscess of its alveolus.*

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Colyer (2) finds that the caries of animals in the wild state usually begin in the dentine or cement, while those of the same animals living in captivity tend to start in the enamel. By way of explanation he postulates that the caries of domestic animals and of wild animals living under domestic conditions are the result of the destruction of the calcium of the enamel by acids derived from fermenting carbohydrates. Animals in the wild state, on the other hand, usually subsist on a diet low in starches and other fermentable carbohydrates and such caries as do occur are probably the secondary result of damage to the enamel permitting lodgement of food under conditions in which direct attack on the dentine or cement is possible.

In the specimen here reported on, there is little indication that the dentine is the primary seat of the decomposition. At only one point is the dentine eroded away so as to undermine the enamel. Rather the destruction of the enamel has preceded the attack upon the dentine. There is evidence, however, that the carious condition is supplemented by an inflammatory decalcification and absorption, involving both crown and roots.

Paradontal Disease

Colyer (2) has pointed out that general destruction of the paradontal tissue is extremely rare in wild-taken ungulates. Usually any such destruction is confined to the alveolus of a single tooth and accompanies an abscessed condition or is directly the result of pressure of food accumulating between malplaced teeth. Present observations confirm the findings of this author. However, there is one specimen, an adult ♀ from Porcher Island, B.C. (B.C.P.M. No. 4559) in which there is pronounced porosity of the alveolar bone together with complete destruction of the interalveolar processes (Fig. 20). This degeneration involves both upper and lower molar rows and the incisiform series and has proceeded to a point that all teeth are loose in their alveoli. There is slight sclerosis upon upper Premolars 3 and 4 on both sides at the alveolar margin.

Discussion of Tooth Anomalies

Despite the facts that the permanent premolars are, in general, shorter anteroposteriorly than the teeth they replace and that their rotation seldom serves to shorten the row, it is difficult to escape the implication that crowding is an important factor in the origin of position anomalies. As has been seen, the teeth that during the course of their development occupy a terminal position, however temporary, are unaffected by this anomaly, whereas premolars 3 and 4, the only teeth that develop in an already circumscribed position, at a time when active elongation of the tooth-bearing region has virtually ceased, are frequently misplaced either with or without rotation.

The frequent presence of vestiges of the deciduous premolar where the permanent premolar is misplaced suggests that this incomplete absorption is in some way associated with the malposition of its permanent successor.

That just two out of eight cases of malposition of the permanent premolars were approximately symmetrical, while all others involved but one member of any given pair of teeth suggests that such displacement was not the direct manifestation of a genetic mutation. On the other hand, all anomalies of form, and two of the three cases of supernumerary teeth, were bilaterally symmetrical, thus strongly suggesting a genetic rather than a mechanical basis for their origin.

Damage to or displacement of any member of the mandibular tooth row frequently leads to the formation of dentoalveolar abscesses. The maxillary row is apparently almost immune to such misfortunes. Possibly the mechanics of jaw action, coupled with the assistance of gravity in compressing food into any interstices in the lower row explains this dissimilarity in the incidence of abscesses.

Irregular attrition frequently, if not usually, accompanies senility and is often responsible for the occurrence of dentoalveolar abscesses.

The single case of caries encountered followed fracture of the enamel. In deer it is most improbable that caries normally form as a result of accumulation of fermentable carbohydrates in depressions in the enamel. Virtually all deer have the central lakes filled with a food mass and yet caries are rare.

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